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HUMES, ARTHUR G. Copepodids and adults of *Leptinogaster major* (Williams, 1907), a poecilostomatoid copepod living in *Mya arenaria* L. and other marine bivalve mollusks 227

MYRICK, A. C., JR., A. A. HOHN, J. BARLOW, and P. A. SLOAN. Reproductive biology of female spotted dolphins, *Stenella attenuata*, from the eastern tropical Pacific .. 247

SYKES, STEPHEN D., and LOUIS W. BOTSFORD. Chinook salmon, *Oncorhynchus tschawytscha*, spawning escapement based on multiple mark-recapture of carcasses 261

PAYNE, P. MICHAEL, JOHN R. NICOLAS, LORETTA O'BRIEN, and KEVIN D. POWERS. The distribution of the humpback whale, *Megaptera novaeangliae*, on Georges Bank and in the Gulf of Maine in relation to densities of the sand eel, *Ammodytes americanus* 271

BAYER, RANGE D. Seabirds near an Oregon estuarine salmon hatchery in 1982 and during the 1983 El Nino 279

WILKINS, MARK E. Development and evaluation of methodologies for assessing and monitoring the abundance of widow rockfish, *Sebastes entomelas* 287

NELSON, WALTER R., and DEAN W. AHRENHOLZ. Population and fishery characteristics of gulf menhaden, *Brevoortia patronus* 311

HAWKES, CLAYTON, R., THEODORE R. MEYERS, and THOMAS C. SHIRLEY. Length-weight relationships of blue, *Paralithodes platypus*, and gulden, *Lithodes aequispina*, king crabs parasitized by the rhizocephalan, *Briarosaccus callosus* Boschma 327

DOHL, THOMAS P., MICHAEL L. BONNELL, and R. GLENN FORD. Distribution and abundance of common dolphin, *Delphinus delphis*, in the Southern California Bight: a quantitative assessment based upon aerial transect data 333

KENNEY, ROBERT D., and HOWARD E. WINN. Cetacean high-use habitats of the northeast United States continental shelf 345

CUMMINGS, WILLIAM C., PAUL O. THOMPSON, and SAMUEL J. HA. Sounds from Bryde, *Balaenoptera edeni*, and finback, *B. physalus*, whales in the Gulf of California 359

PEREZ, MICHAEL A., and ELIZABETH E. MOONEY. Increased food and energy consumption of lactating northern fur seals, *Callorhinus ursinus* 371

BIGG, MICHAEL A. Arrival of northern fur seals, *Callorhinus ursinus*, on St. Paul Island, Alaska 383

(Continued on back cover)

Seattle, Washington

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Fishery Bulletin

CONTENTS

Vol. 84, No. 2 April 1986

HUMES, ARTHUR G. Copepodids and adults of *Leptinogaster major* (Williams, 1907), a poecilostomatoid copepod living in *Mya arenaria* L. and other marine bivalve mollusks 227
MYRICK, A. C., JR., A. A. HOHN, J. BARLOW, and P. A. SLOAN. Reproductive biology of female spotted dolphins, *Stenella attenuata*, from the eastern tropical Pacific .. 247
SYKES, STEPHEN D., and LOUIS W. BOTSFORD. Chinook salmon, *Oncorhynchus tschawytscha*, spawning escapement based on multiple mark-recapture of carcasses 261
PAYNE, P. MICHAEL, JOHN R. NICOLAS, LORETTA O'BRIEN, and KEVIN D. POWERS. The distribution of the humpback whale, *Megaptera novaeangliae*, on Georges Bank and in the Gulf of Maine in relation to densities of the sand eel, *Ammodytes americanus* 271
BAYER, RANGE D. Seabirds near an Oregon estuarine salmon hatchery in 1982 and during the 1983 El Nino 279
WILKINS, MARK E. Development and evaluation of methodologies for assessing and monitoring the abundance of widow rockfish, *Sebastes entomelas* 287
NELSON, WALTER R., and DEAN W. AHRENHOLZ. Population and fishery characteristics of gulf menhaden, *Brevoortia patronus* 311
HAWKES, CLAYTON, R., THEODORE R. MEYERS, and THOMAS C. SHIRLEY. Length-weight relationships of blue, *Paralithodes platypus*, and golden, *Lithodes aequispina*, king crabs parasitized by the rhizocephalan, *Briarosaccus callosus* Boschma 327
DOHL, THOMAS P., MICHAEL L. BONNELL, and R. GLENN FORD. Distribution and abundance of common dolphin, *Delphinus delphis*, in the Southern California Bight: a quantitative assessment based upon aerial transect data 333
KENNEY, ROBERT D., and HOWARD E. WINN. Cetacean high-use habitats of the northeast United States continental shelf 345
CUMMINGS, WILLIAM C., PAUL O. THOMPSON, and SAMUEL J. HA. Sounds from Bryde, *Balaenoptera edeni*, and finback, *B. physalus*, whales in the Gulf of California 359
PEREZ, MICHAEL A., and ELIZABETH E. MOONEY. Increased food and energy consumption of lactating northern fur seals, *Callorhinus ursinus* 371
BIGG, MICHAEL A. Arrival of northern fur seals, *Callorhinus ursinus*, on St. Paul Island, Alaska 383

(Continued on next page)

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1986

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LO, NANCY C. H. Modeling life-stage-specific instantaneous mortality rates, an application to northern anchovy, *Engraulis mordax*, eggs and larvae 395
SEN, A. R. Methodological problems in sampling commercial rockfish landings ... 409
POLOVINA, JEFFREY J. A variable catchability version of the Leslie model with application to an intensive fishing experiment on a multispecies stock 423
MATSUURA, YASUNOBU, and NELSON TAKUMI YONEDA. Early development of the lophid anglerfish, *Lophius gastrophysus* 429
SQUIRES, DALE. Ex-vessel price linkages in the New England fishing industry .. 437
LEBER, KENNETH M., and HOLLY S. GREENING. Community studies in seagrass meadows: A comparison of two methods for sampling macroinvertebrates and fishes 443

Notes

OXENFORD, HAZEL A., and WAYNE HUNTE. A preliminary investigation of the stock structure of the dolphin, *Coryphaena hippurus*, in the western central Atlantic 451
FORWARD, RICHARD B., JR., BLANCA ROJAS de MENDIOLA, and RICHARD T. BARBER. Effects of temperature on swimming speed of the dinoflagellate *Gymnodinium splendens* 460
GRAHAM, JEFFREY B., RICHARD H. ROSENBLATT, and DARCY L. GIBSON. Morphology and possible swimming mode of a yellowfin tuna, *Thunnus albacares*, lacking one pectoral fin 463
RATTY, F. J., Y. C. SONG, and R. M. LAURS. Chromosomal analysis of albacore, *Thunnus alalunga*, and yellowfin, *Thunnus albacares*, and skipjack, *Katsuwonus pelamis*, tuna 469
STIER, KATHLEEN, and BOYD KYNARD. Abundance, size, and sex ratio of adult sea-run sea lamprey, *Petromyzon marinus*, in the Connecticut River 476
MASON, J. C., and A. C. PHILLIPS. An improved otter surface sampler 480
GROVER, JILL J., and BORI L. OLLA. Morphological evidence for starvation and prey size selection of sea-caught larval sablefish, *Anoplopoma fimbria* 484
Notices 490

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COPEPODIDS AND ADULTS OF *LEPTINOGASTER MAJOR* (WILLIAMS, 1907), A POECILOSTOMATOID COPEPOD LIVING IN *MYA ARENARIA* L. AND OTHER MARINE BIVALVE MOLLUSKS

ARTHUR G. HUMES[1]

ABSTRACT

The five copepodid stages and adults of *Leptinogaster major* (Williams, 1907), a poecilostomatoid copepod (family Clausidiidae) living in the mantle cavity of *Mya arenaria* L. and other marine bivalve mollusks along the coast of eastern North America from Prince Edward Island, Canada, to Louisiana, are described. Copepodid I is *Saphirella*-like in body form. In the adult female the maxilliped is present though much reduced. Sexual differentiation first occurs in Copepodid IV, where the male and female maxillipeds are differently formed.

The poecilostomatoid copepod *Leptinogaster* (= *Myocheres*) *major* (Williams, 1907) has been reported from the mantle cavity of various marine bivalve mollusks along the eastern shore of North America, from Prince Edward Island, Canada (J. C. Medcof in correspondence with M. S. Wilson) to Louisiana (Causey 1953). This copepod has undergone several name changes, but it seems generally agreed now that it properly belongs in the genus *Leptinogaster* (see Bocquet and Stock 1958, and Table 1). The seasonal population changes and host relationships of this species have been described by Humes and Cressey (1960), who listed as hosts *Mya arenaria* L., *Tagelus gibbus* (Spengler), *Venus mercenaria* L., and *Ensis directus* (Conrad). Other hosts include *Mactra solidissima* Dillwyn (reported by Williams 1907), *Dosinia gibbus* Reeve (reported by Pearse 1947), and *Pholas costata* L. (reported by Causey 1953). For a list of bivalve hosts and localities see Table 2.

The copepodid development of *Leptinogaster* has not been fully described. Bocquet and Stock (1958) mentioned finding copepodids of *Leptinogaster histrio* (Pelseneer 1929) and figured the maxillipeds of an unknown stage (their fig. 3d, e); they also reported a Copepodid V of *Leptinogaster* sp. and il-

TABLE 1.—Taxonomic history of *Leptinogaster major* (Williams, 1907).

Lichomolgus major Williams, 1907, p. 77, pl. III, 8 figs.; Sharpe 1910, p. 408, placed in Lichomolgidae.
Myicola major, C. B. Wilson, 1932, p. 347, fig. 208, genus wrongly assigned; Monod and Dollfus 1934, p. 316, placed in Clausiidae; Deevey 1948, p. 22, 1960, p. 34; Sewell 1949, p. 156, placed in Lichomolgidae; Causey 1953, p. 12.
Myicola spinosa Pearse, 1947, p. 5, figs. 26-31, placed in Myicolidae.
Myocheres major, M. S. Wilson, 1950, p. 299; M. S. Wilson and Illg 1955, p. 136, 138; Allen 1956, p. 62, placed tentatively in Lichomolgidae; Bocquet and Stock 1957a, p. 213, 221, placed in Clausidiidae; Humes and Cressey 1958, p. 932, 934, placed in Clausidiidae; Băcescu and Por 1959, p. 20, placed in Clausidiidae; Humes and Cressey 1960, p. 307-325.
Leptinogaster major, Bocquet and Stock, 1958, p. 86-88, placed in Clausidiidae; Gooding 1963, p. 132-136, pl.17, figs. a-n.

TABLE 2.—Localities and hosts of *Leptinogaster major*.

Locality	Host(s)	Source
Ellerslie, Prince Edward Island, Can.	*Mya arenaria* L.	J. C. Medcof in correspondence (23 May 1950) with M. S. Wilson
Bideford River, Prince Edward Island, Can.	*Mya arenaria* L.	J. C. Medcof in correspondence (31 July 1948) with M. S. Wilson
Cotuit, MA	*Mya arenaria* L. *Tagelus gibbus* (Spengler) *Venus mercenaria* L. *Ensis directus* (Conrad)	Humes and Cressey (1960)
Marthas Vineyard, MA	in plankton	Deevey (1948)
Wickford and Matunuck, RI	*Mya arenaria* L. *Venus mercenaria* L. *Mactra solidissima* Dillwyn	Williams (1907)
Delaware Bay	in plankton	Deevey (1960)
Beaufort, NC	*Tagelus gibbus* (Spengler) *Dosinia discus* Reeve *Venus mercanaria* L.	Pearse (1947)
Grand Isle, LA	*Pholas costata* L.	Causey (1953)

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lustrated its maxilliped (their fig. 6b, c). Gooding (1963) described features of Copepodid I of *Leptinogaster major*.

Before her death Mildred S. Wilson had studied specimens of *Leptinogaster* (= *Myocheres*) *major* that had been sent to her from Rhode Island and Prince Edward Island, and had prepared the first draft of a redescription. She recognized the need for a thorough redescription of this species whose original description by Williams (1907) is very incomplete. Although she wrote (1950) that a detailed description of adults and developmental forms was then in preparation, this study apparently was never completed. In a letter to J. C. Medcof dated 24 August 1948 she stated that she had found two early stages of *Myocheres*. Presumably descriptions of these copepodids would have been part of her projected study if she had lived.

During the study by Humes and Cressey (1960) a large number of *Leptinogaster major* (1,535) were collected from *Mya arenaria* over a period of almost 2 yr at Cotuit, MA. The copepodids and adults described below came from collections made during the summer of 1957. All five copepodid stages, distinguished on the basis of the number of body segments, as well as adults, were obtained. This paper deals with the detailed description of the external morphology of these immature stages and adults.

Although the copepodids described here were not obtained by rearing, it seems certain that the copepodids found in such large numbers are those of *Leptinogaster major*. No other species of copepods occurred in the *Mya arenaria* examined.

MATERIALS AND METHODS

The copepodids and adults described here were selected from a pool of 305 copepodids and 195 adults found in 125 *Mya arenaria* during May-September at Cotuit, MA. The successive Copepodids I-V and the adults were cleared in lactic acid and sorted by size and external morphology into their respective groups.

All measurements and dissections were made on specimens cleared in lactic acid, following the method of Humes and Gooding (1964). The body length does not include the setae on the caudal rami. The measurements of certain parts, such as the length of the first antenna, maxilliped, and various setae and claws, and the dimensions of leg 5, the caudal ramus, and the urosomal segments, are based on dissected specimens from which the drawings were made, and may be considered representative of nearly average body size. Such measurements are intended more to show relative changes in size during successive instars rather than to represent absolute size. The drawings were made with the aid of a camera lucida. The abbreviations used are as follows: A_1 = first antenna, A_2 = second antenna, L = labrum, MD = mandible, MX_1 = first maxilla, MX_2 = second maxilla, P_3 = leg 3, P_4 = leg 4, and P_5 = leg 5.

DESCRIPTIONS

Copepodid I

Figures 1a-n, 2a-c

Size.—Length 0.57 mm (0.45-0.60 mm) and greatest width 0.17 mm (0.16-0.18 mm) based on 38 specimens.

Body form (Fig. 1a, b, c).—*Saphirella*-like, with cephalosome bluntly pointed anteriorly. Five body segments including and posterior to segment bearing leg 1. Anal segment with 4 groups of spines, 2 ventral groups and 2 ventrolateral groups (Fig. 1d).

Caudal ramus (Fig. 1e).—Relatively short, 36 × 18 μm, ratio 2:1, with 6 setae. Outer lateral seta 18 μm, dorsal seta 20 μm, 4 terminal setae from outer to inner 23, 17, 39, and 176 μm, the last with minute lateral spinules.

Rostrum (Fig. 1f).—Broad ridge, prominent in lateral view (Fig. 1g).

First antenna (Fig. 1h).—Five-segmented, 83 μm long. Armature: 2, 2, 3 + 1 aesthete, 2 + 1 aesthete, and 5 + 1 aesthete. All setae smooth.

Second antenna (Fig. 1i).—Indistinctly 4-segmented, last segment obscure. First segment with 1 distal seta. Second segment with 1 seta and group of small spines. Third segment with outer row of spines and 2 slender inner setules, with outer stout curved seta having expanded serrate distal half and 1 short inner blunt seta. Fourth segment small and indistinctly set off from third segment, with 1 blunt short seta, 1 long stout smooth seta, 1 slender smooth seta, and 1 long stout seta with prominent lateral setules.

Labrum (Fig. 1j).—Broad, with ventral surface bearing 2 medially interrupted rows of spines and with posteroventral margin having row of small

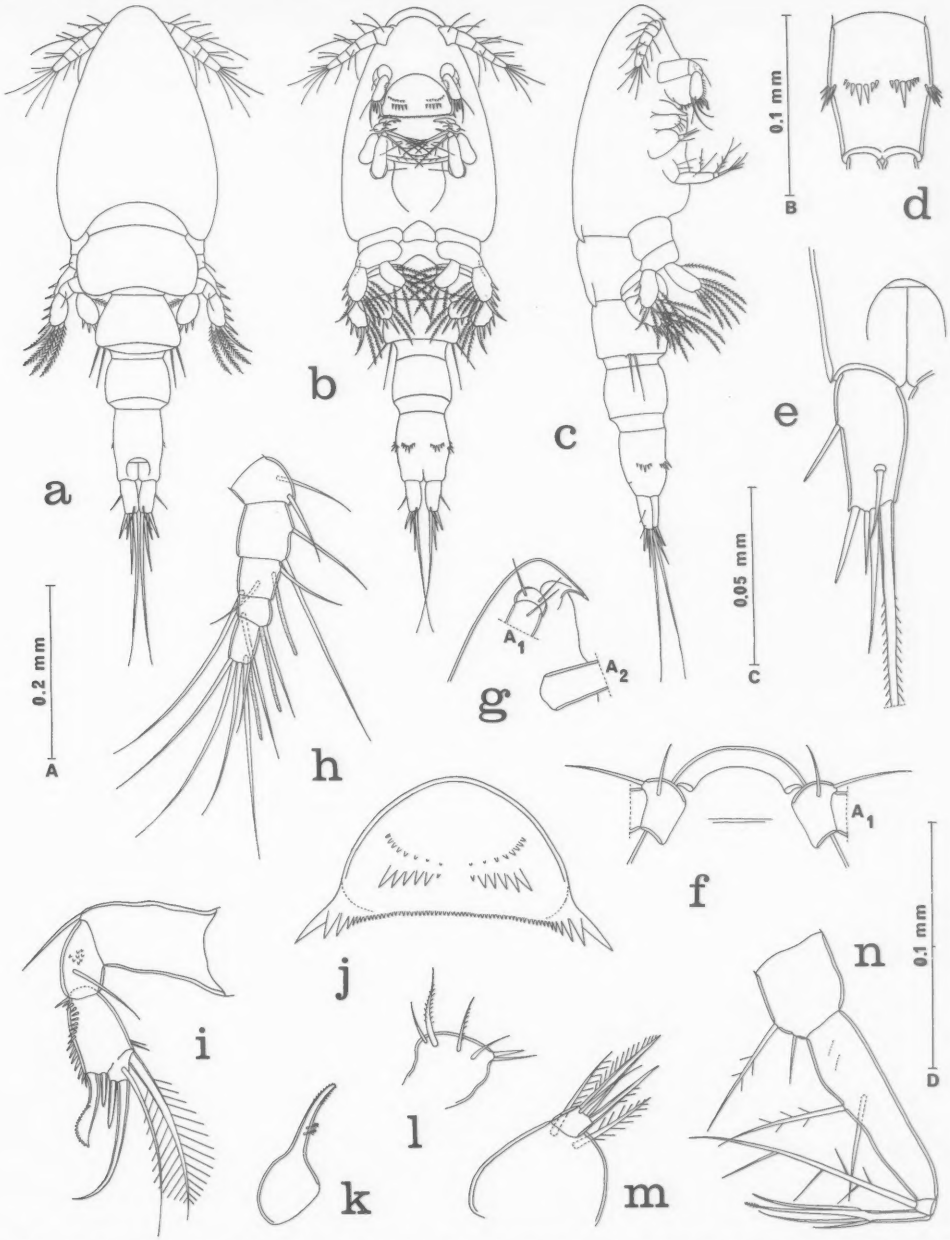

FIGURE 1.—Copepodid I of *Leptinogaster major*: a, dorsal (scale A); b, ventral (A); c, lateral (A); d, anal segment, ventral (B); e, caudal ramus, dorsal (C); f, rostral area, ventral (D); g, rostral area, lateral (B); h, first antenna, dorsal (D); i, second antenna, dorsal (C); j, labrum, in situ, ventral (C); k, mandible, ventral (C); l, first maxilla, ventral (C); m, second maxilla, ventral (C); n, maxilliped, posterior (C).

spines, these spines becoming much larger at both corners.

Mandible (Fig. 1k).—Simple form, small, about 42 μm long, with expanded base but slender distal portion bearing 2 minute setae midway and having minutely pectinate tip.

Paragnath.—Minute smooth lobe.

First maxilla (Fig. 1l).—Small lobe bearing 6 setae.

Second maxilla (Fig. 1m).—Two-segmented, large first segment with 2 setae, small second segment with 3 setae.

Maxilliped (Fig. 1n).—Elongate, slender, 4-segmented. First segment with 2 setae. Elongate second segment with 2 setae and 2 small setules. Small third segment with 1 long seta having few prominent lateral setules. Fourth segment bearing 3 setae near midregion and extended beyond as setiform process with few minute barbs near tip.

Leg 1 (Fig. 2a).—Both rami 1-segmented. Formula for armature: coxa 0-0; basis 1-0; exopod III,I,4; endopod 1,5,1. Exopod with 3 outer spines having prominent lateral spinules and terminal outer spine and adjacent seta with outer denticulations.

Leg 2 (Fig. 2b).—Both rami 1-segmented. Armature: coxa 0-0; basis 1-0; exopod III,I,3; endopod III,2,1. Exopod spines with lateral spinules or denticulations as in leg 1; endopod spines finely barbed.

Leg 3 (Fig. 2c).—Consisting of 2 setae, 70 and 57 μm, with 2 very small spines near their insertions.

Legs 4, 5, and 6.—Absent.

Copepodid II

Figures 2d-m, 3a-e

Size.—Length 0.68 mm (0.59-0.72 mm) and greatest width 0.19 mm (0.18-0.20 mm), based on 31 specimens.

Body form (Fig. 2d).—No longer *Saphirella*-like. Suggesting form of later instars. Six body segments including and posterior to segment bearing leg 1. Segment bearing leg 4 ventrally with 2 transverse rows of spines (Fig. 2e). Anal segment ventrally with distal spines in addition to 4 groups of proximal spines. Ventrolateral areas of cephalosome at level of mouthparts with strip of small spinules (Fig. 3a).

Caudal ramus.—Similar to Copepodid I but few small ventral spines distally.

Rostrum (Fig. 2f).—Suggesting rounded form seen in later instars.

First antenna (Fig. 2g).—Five-segmented, 107 μm long. Armature: 2, 3, 3 + 1 aesthete, 2 + 1 aesthete, and 6 + 1 aesthete.

Second antenna (Fig. 2h).—Four-segmented. Third segment with 2 strong recurved outer clawlike spines. Small fourth segment with 4 smooth setae, 2 middle setae curved.

Labrum (Fig. 2i).—Posteroventral margin sharply pointed. No surficial or marginal ornamentation.

Mandible (Fig. 2j).—Elongate, 43 μm, distally with 3 elements, 2 helmet-shaped and 1 stoutly spiniform, all with minute marginal barbs.

Paragnath.—As an adult (see Fig. 7f).

First maxilla (Fig. 2k).—Small lobe bearing 5 setae.

Second maxilla (Fig. 2l).—Two-segmented, its form suggesting later instars. First segment expanded with outer patch of small spines. Second segment clawlike, 30 μm long, with 1 inner seta.

Maxilliped (Fig. 2m).—Delicately sclerotized and weakly 4-segmented, length 40 μm. Relative positions of maxillipeds and head appendages as in Figure 3a.

Leg 1 (Fig. 3b).—Both rami 2-segmented. Armature: coxa 0-0; basis 1-I; exopod I-0; III,5; endopod 0-1; I,5.

Leg 2 (Fig. 3c).—Both rami 2-segmented. Armature: coxa 0-0; basis 1-0; exopod I-0; III,4; endopod 0-1; III,3.

Leg 3 (Fig. 3d).—Both rami 1-segmented. Armature: coxa 0-0; basis 1-0; exopod III,4; endopod III,3.

Leg 4 (Fig. 3e).—Consisting of 2 setae, 52 and 39 μm.

Legs 5 and 6.—Absent.

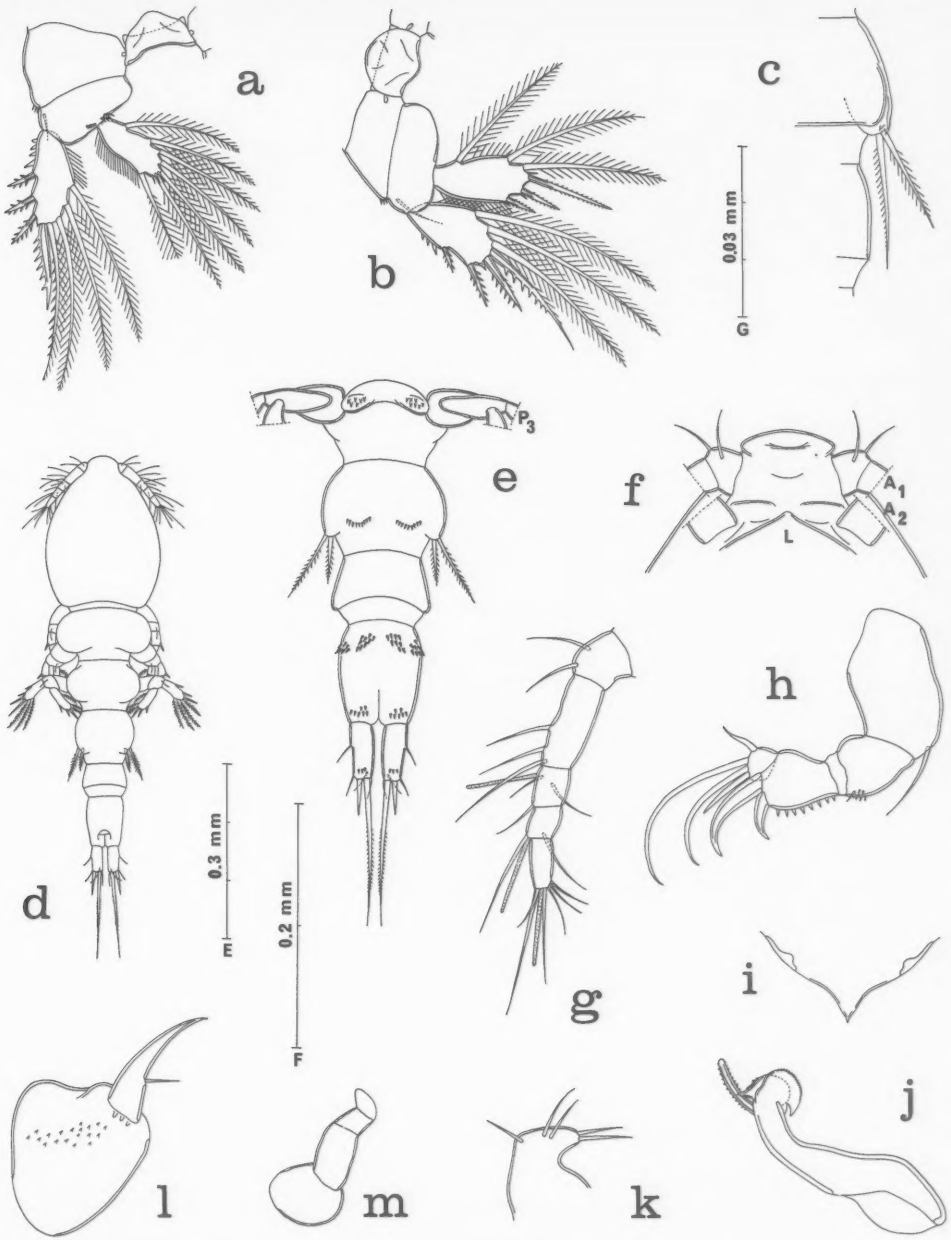

FIGURE 2.—Copepodid I of *Leptinogaster major*, a-c: a, leg 1 and intercoxal plate, anterior (scale B); b, leg 2 and intercoxal plate, anterior (B); c, leg 3, dorsal (B). Copepodid II of *Leptinogaster major*, d-m: d, dorsal (E); e, body posterior to leg 4, ventral (F); f, rostral area, ventral (B); g, first antenna, dorsal (D); h, second antenna, anteromesial (C); i, labrum, ventral (D); j, mandible, ventral (G); k, first maxilla, anterior (C); l, second maxilla, posteroventral (C); m, maxilliped (C).

Copepodid III

Figures 3f-k, 4a-d

Size.—Length 0.85 mm (0.72-0.95 mm) and greatest width 0.24 mm (0.21-0.26 mm), based on 37 specimens.

Body form (Fig. 3f).—Spinules on ventral surface of segment of leg 5 (Fig. 3g) continuous across segment. Seven body segments including and posterior to segment bearing leg 1. (One specimen, 0.62 × 0.24 mm, with segments behind leg 4 telescoped as in Figure 3h.)

First antenna (Fig. 3i).—Five-segmented, 145 μm long. Armature: 3, 10, 3 + 1 aesthete, 2 + 1 aesthete, and 7 + 1 aesthete.

Second antenna (Fig. 3j).—Similar to Copepodid II but outermost seta on fourth segment longer and recurved.

Maxilliped.—As in Copepodid II.

Leg 1 (Fig. 3k).—Both rami 2-segmented. Armature: coxa 0-0, basis 1-I; exopod I-0; III, 5; endopod 0-1; I,6.

Leg 2 (Fig. 4a).—Both rami 2-segmented. Armature: coxa 0-0; basis 1-0; exopod I-0; III,6; endopod 0-1; III,4.

Leg 3 (Fig. 4b).—Both rami 2-segmented. Armature: coxa 0-0, basis 1-0; exopod 0-1; II,5; endopod 0-1; III,3.

Leg 4 (Fig. 4c).—Both rami 1-segmented. Armature: coxa 0-0; basis 1-0; exopod II,4; endopod III,3. (Distal outer seta on exopod somewhat spiniform.)

Leg 5 (Fig. 4d).—Represented by 2 setae, 42 and 29 μm.

Leg 6.—Absent.

Copepodid IV, female

Figures 4e-k, 5a-c

Size.—Length 1.19 mm (0.93-1.33 mm) and greatest width 0.32 mm (0.28-0.35 mm), based on 42 specimens.

Body form (Fig. 4e).—Eight body segments including and posterior to segment bearing leg 1. Spinules on ventral surface of segment bearing leg 5 and on anal segment (Fig. 4f) as in Copepodid III.

First antenna (Fig. 4g).—Five-segmented, 179 μm long, but slight notch on posterior edge of second segment suggesting division of segment. Armature: 4, 15, 4 + 1 aesthete, 2 + 1 aesthete, and 7 + 1 aesthete.

Maxilliped (Fig. 4h).—Two-segmented, weakly sclerotized, distal segment lobelike. Relative position of maxillipeds as in Figure 4i.

Leg 1.—Both rami 2-segmented. Armature (as in Copepodid III): coxa 0-0; basis 1-0; exopod I-0; III,5; endopod 0-1; I,6.

Leg 2 (Fig. 4j).—Both rami 2-segmented. Armature: coxa 0-0; basis 1-0; exopod I-0; III,6; endopod 0-1; II,6. Distalmost outer seta on endopod somewhat spiniform.

Leg 3 (Fig. 4k).—Both rami 2-segmented. Armature: coxa 0-0; basis 1-0; exopod I-0; III,6; endopod 0-1; II,5. Distalmost outer seta on endopod somewhat spiniform.

Leg 4 (Fig. 5a).—Both rami 2-segmented. Armature: coxa 0-0; basis 1-0; exopod I-0; III,5; endopod 0-1; III,3.

Leg 5 (Fig. 5b).—Two-segmented, but first segment, armed with 1 seta, not clearly set off from body; second segment oval, 60 × 30 μm, bearing 3 spines and 1 seta, with few small spinules near insertion of proximalmost and distalmost spines.

Leg 6 (Fig. 5c).—Represented by 1 seta 32 μm long, with minute spinules near insertion.

Copepodid IV, male

Figure 5d-g

Size.—Length 1.07 mm (0.90-1.19 mm) and greatest width 0.28 mm (0.25-0.31 mm), based on 38 specimens.

Body form.—As in female, with same number of body segments and similar arrangement of ventral spinules (Fig. 5d).

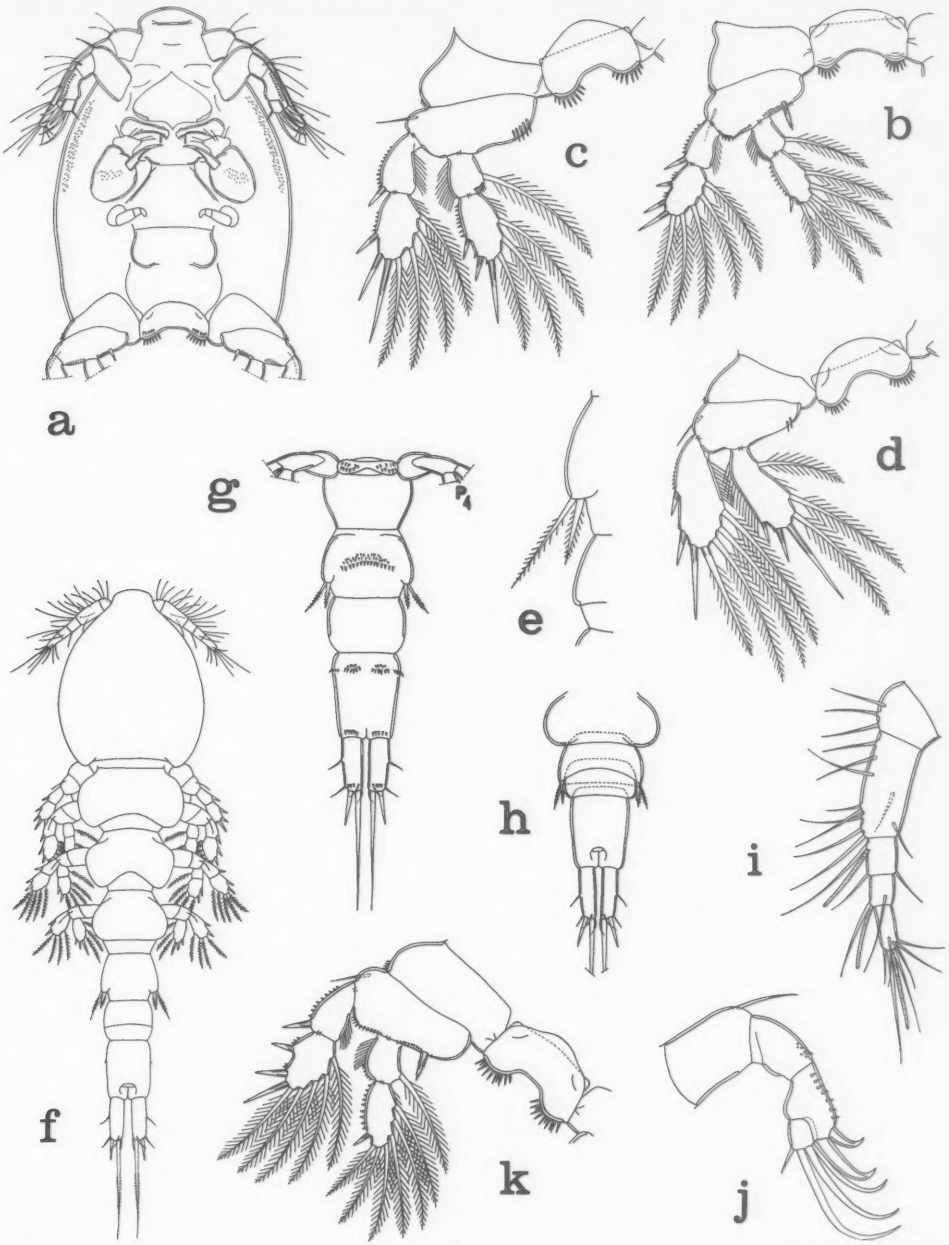

FIGURE 3.—Copepodid II of *Leptinogaster major*, a-e: a, cephalosome, ventral (scale F); b, leg 1 and intercoxal plate, anterior (B); c, leg 2 and intercoxal plate, anterior (B); d, leg 3 and intercoxal plate, anterior (B); e, leg 4, ventral (B). Copepodid III of *Leptinogaster major*, f-k: f, dorsal (E); g, body posterior to leg 4, ventral (A); h, posterior part of body showing telescoped segments, dorsal (A); i, first antenna, ventral (B); j, second antenna, anteromesial (D); k, leg 1 and intercoxal plate, anterior (B).

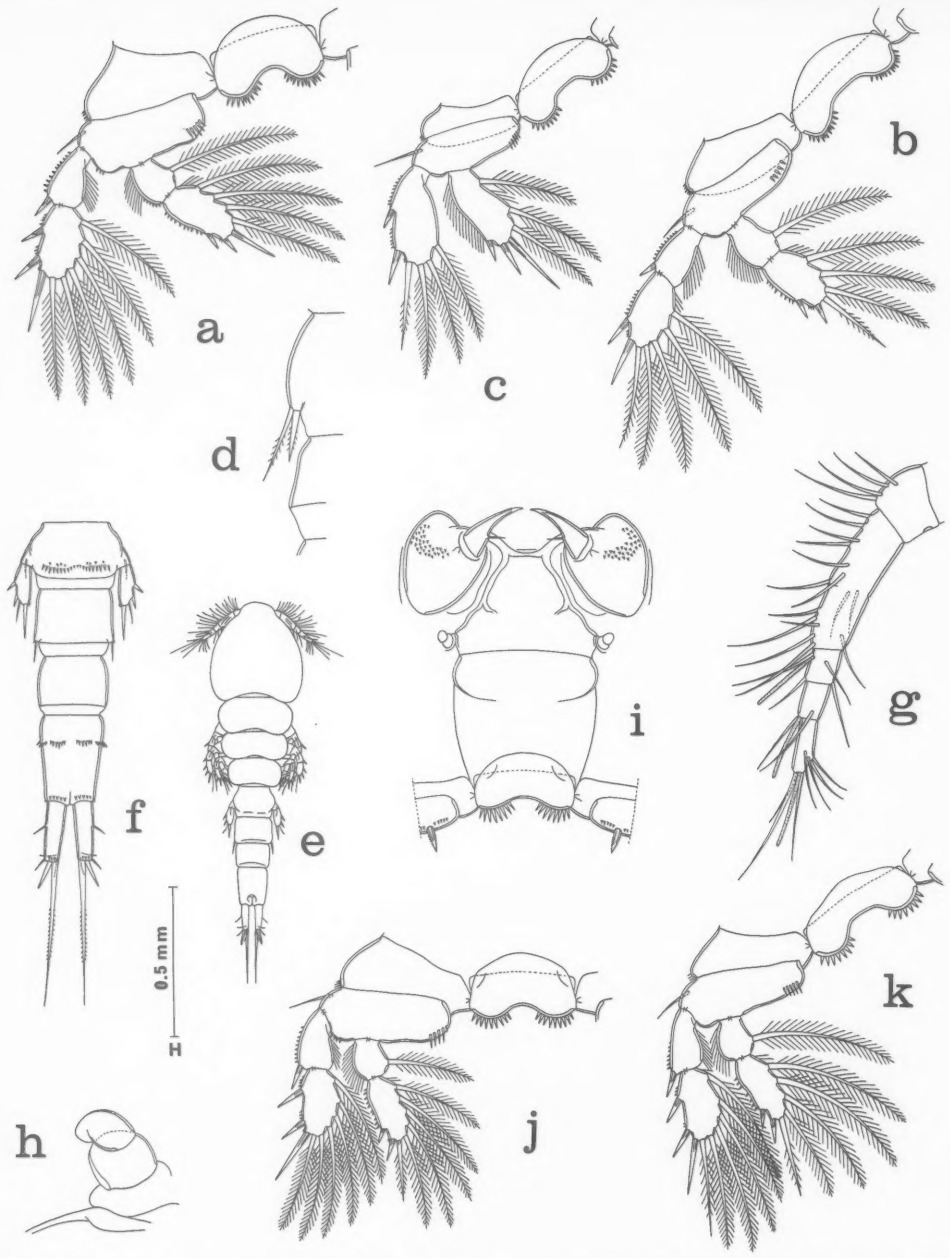

FIGURE 4.—Copepodid III of *Leptinogaster major*, a-d: a, leg 2 and intercoxal plate, anterior (scale B); b, leg 3 and intercoxal plate, anterior (B); c, leg 4 and intercoxal plate, anterior (B); d, leg 5, ventral (B). Copepodid IV of *Leptinogaster major*, female, e-k: e, dorsal (H); f, urosome, ventral (E); g, first antenna, ventral (B); h, maxilliped, ventral (C); i, ventral region from second maxillae to first pair of legs, showing maxillipeds (F); j, leg 2 and intercoxal plate, anterior (F); k, leg 3 and intercoxal plate, anterior (F).

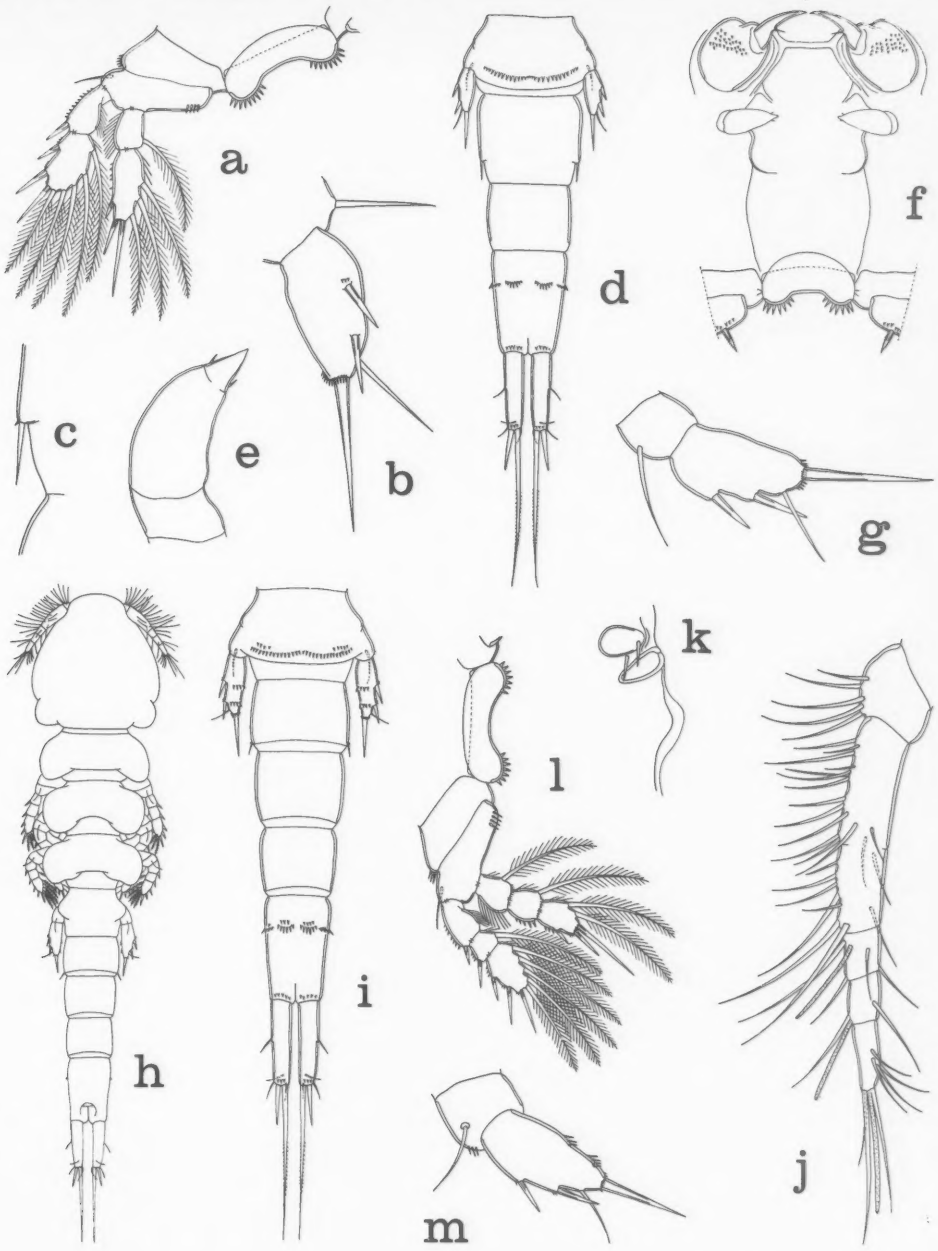

FIGURE 5.—Copepodid IV of *Leptinogaster major*, female a-c: a, leg 4 and intercoxal plate, anterior (scale F); b, leg 5, lateral (D); c, leg 6, ventral (D); male, d-g: d, urosome, ventral (A); e, maxilliped, ventral (C); f, ventral region from second maxillae to first pair of legs, showing maxillipeds (F); g, leg 5, dorsal (D). Copepodid V of *Leptinogaster major*, female, h-m: h, dorsal (H); i, urosome, ventral (E); j, first antenna, posteroventral (B); k, maxilliped, ventral (C); l, leg 4 and intercoxal plate, anterior (A); m, leg 5, dorsal (F).

Maxilliped (Fig. 5e).—Three-segmented, 50 μm long, with small pointed third segment weakly set off from second segment and bearing 2 small setae. Relative position of maxillipeds as in Figure 5f.

Leg 5 (Fig. 5g).—Two-segmented. First segment set off from body. Second segment 55 × 29 μm. Armature similar to female.

Leg 6 (Fig. 5d).—Represented by single seta.

Copepodid V, female

Figures 5h-m, 6a-c

Size.—Length 1.62 mm (1.42-1.87 mm) and greatest width 0.41 mm (0.37-0.44 mm), based on 13 specimens.

Body form (Fig. 5h).—Nine body segments including and posterior to segment bearing leg 1. Segment of leg 5 and more posterior segments as in Figure 5i.

Caudal ramus (Fig. 5i).—Noticeably longer than in preceding instars.

First antenna (Fig. 5j).—Incompletely 6-segmented. Armature: 5, 15 + 9, 4 + 1 aesthete, 2 + 1 aesthete, and 7 + 1 aesthete.

Maxilliped (Fig. 5k).—Reduced to slightly raised lobe with 2 small setae.

Leg 1.—Both rami 3-segmented. Armature (as in adult): coxa 0-0; basis 1-I; exopod I-0; I-1; III,5; endopod 0-1, 0-1; I,5.

Legs 2 and 3.—Both rami 3-segmented. Armature (as in adult): coxa 0-0; basis 1-0; exopod I-0; I-1; III,6; endopod 0-1; 0-2; III,3.

Leg 4 (Fig. 5l).—Both rami 3-segmented. Armature: coxa 0-0, basis 1-0; exopod I-0; I-1; III,5; endopod 0-1; 0-1; III,2. Distalmost spine on exopod more slender than other exopod spines; outer of 2 terminal spines on endopod only about one-half length of inner terminal spine.

Leg 5 (Fig. 5m).—Second segment 99 × 49 μm. Few outer spinules on first segment. Two groups of spinules on inner side of second segment. Principal armature as in Copepodid IV.

Leg 6 (Fig. 5i).—Represented by 1 seta with minute spinule near its insertion.

Copepodid V, male

Figure 6a-c

Size.—Length 1.41 mm (1.22-1.57 mm) and greatest width 0.34 mm (0.31-0.39 mm), based on 30 specimens.

Body form.—As in female, with same number of body segments. Similar arrangement of ventral spinnules on urosomal segments (Fig. 6a).

Maxilliped (Fig. 6b).—Four-segmented. First segment with 1 inner seta. Long second segment and short third segment unarmed. Pointed fourth segment with 2 setae.

Legs 1-4.—Similar to those of female. Endopod of leg 2 (Fig. 6c) not showing sexual dimorphism.

Leg 5.—As in female; second segment 75 × 31 μm.

Leg 6.—Represented by single seta with few very small spinules near its insertion.

Adult Female

Figures 6d-m, 7a-l, 8a-e, 9a-j

Size.—Length 2.18 mm (1.92-2.45 mm) and greatest width 0.52 mm (0.47-0.56 mm), based on 10 specimens. Dorsoventral thickness at level of leg 1, 0.25 mm.

Body form (Fig. 6d, e).—Elongate and flattened dorsoventrally. Nine body segments including and posterior to segment bearing leg 1. Urosome 5-segmented (Fig. 6f). Segment bearing leg 5 220 × 319 μm in dorsal view, smooth on dorsal surface, but ventral surface with transverse groups of spines (Fig. 6g); dorsally this segment with posterodorsal hump (Fig. 6e, h). Genital segment 270 × 264 μm, wider in anterior half than in posterior half. Three postgenital segments from anterior to posterior 143 × 165, 143 × 160, and 200 × 143 μm. Genital areas situated dorsolaterally, each area (Fig. 6i) bearing 2 very small setae about 16 μm long. Ventral surfaces of genital segment and first and second postgenital segments smooth. Anal segment ventrally with few small spines at postero-outer corners, with row of 5 spines on each side distally, and with 2

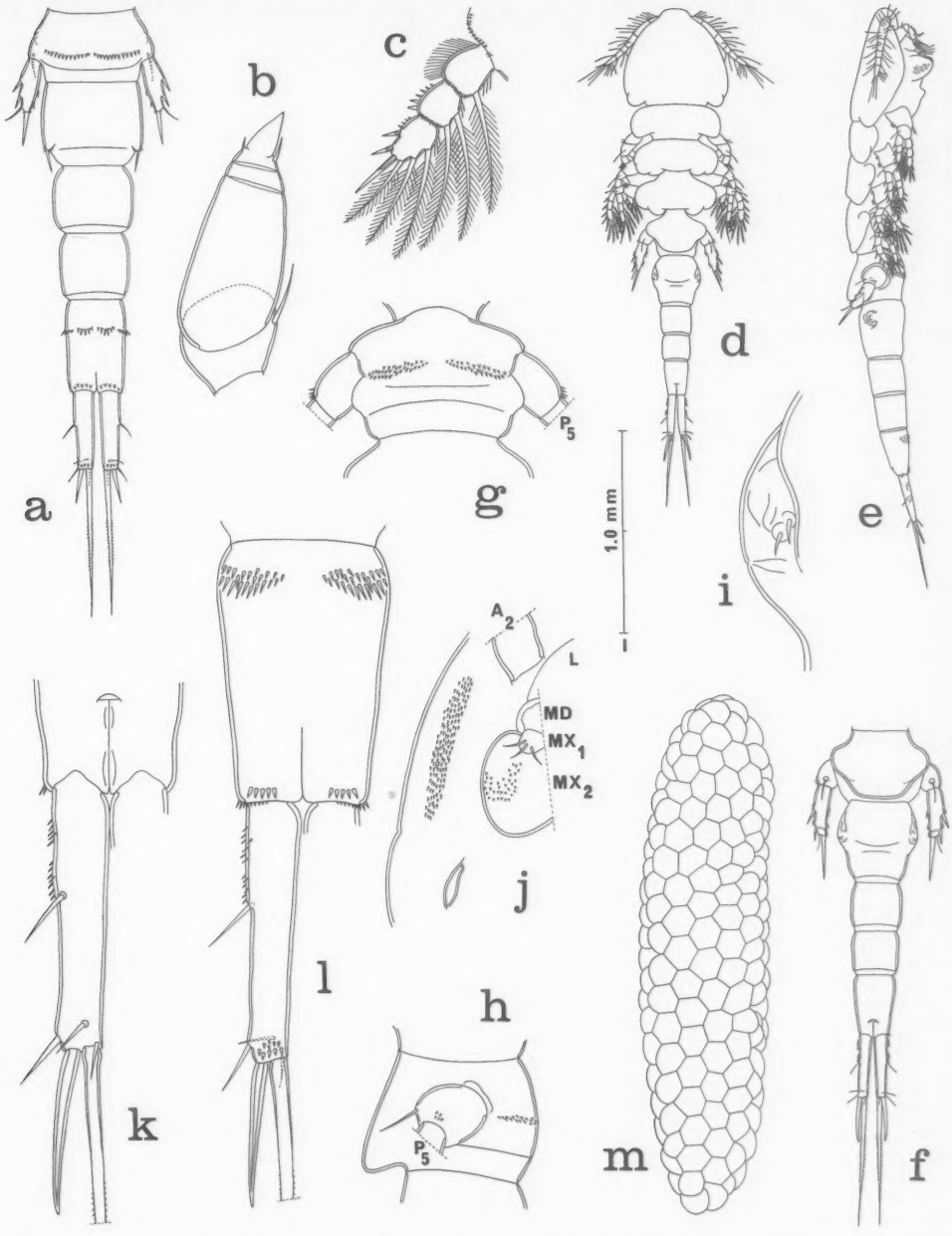

FIGURE 6.—Copepodid V of *Leptinogaster major*, male, a-c: a, urosome, ventral (scale E); b, maxilliped, ventral (D); c, endopod of leg 2, anterior (F). Adult female of *Leptinogaster major*, d-m: d, dorsal (I), e, lateral (I); f, urosome, dorsal (H); g, segment bearing fifth pair of legs, ventral (A); h, segment bearing leg 5, lateral (E); i, genital area, dorsal (B); j, patch of spinules and sclerotized area on side of cephalosome, ventral (E); k, caudal ramus, dorsal (F); l, anal segment and caudal ramus, ventral (F); m, egg sac, ventral (E).

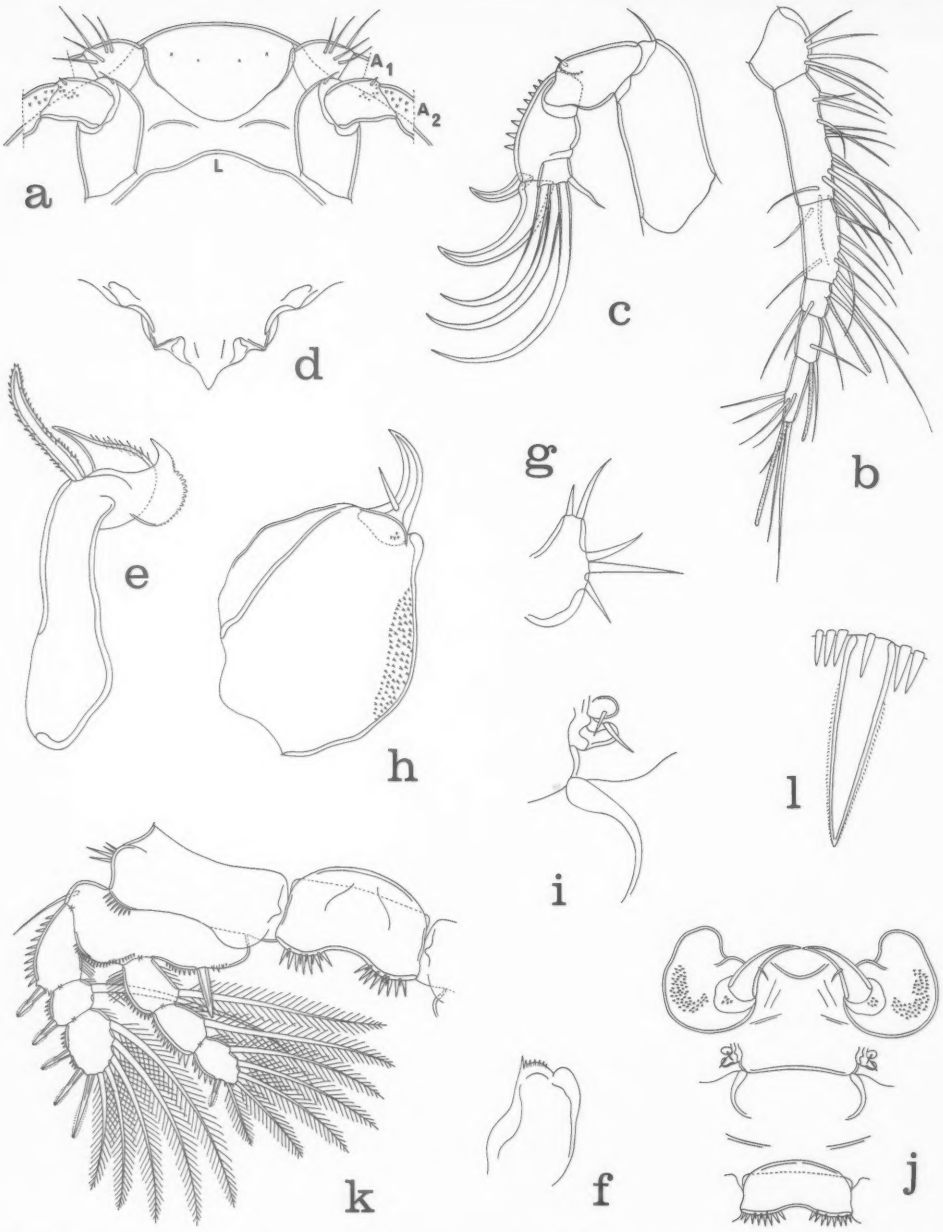

FIGURE 7.—Adult female of *Leptinogaster major*: a, rostrum, ventral (scale F); b, first antenna, posteroventral (F); c, second antenna, posteromesial (B); d, labrum, ventral (B); e, mandible, anteroventral (C); f, paragnath, ventral (D); g, first maxilla, anterior (D); h, second maxilla, posterior (B); i, maxilliped, ventral (D); j, ventral region from second maxillae to first pair of legs, showing maxillipeds (E); k, leg 1 and intercoxal plate, anterior (F); l, inner spine on basis of leg 1, anterior (G).

prominent groups of spines anteriorly. Cephalosome ventrally with elongate oblique strip of small spines between edge of body and region of mouthparts, and with small elongate oval sclerotized area lateral to level of maxillipeds (Fig. 6j).

Caudal ramus (Fig. 6k, l).—Elongate, 221 μm long, greatest width 44 μm, least width 35 μm, ratio about 5.5:1. Outer lateral seta 50 μm. Dorsal seta 26 μm. Outermost terminal seta 52 μm. Innermost terminal seta 26 μm. Outer of 2 median terminal setae 130 μm and almost spinelike. Inner of 2 median terminal seta 440 μm, with extremely small lateral spinules. Other setae smooth. Outer margin of ramus proximal to outer lateral seta with 2 groups of spinules. Distal end of ramus ventrally with patch of small spines.

Egg sac (Fig. 6m).—Elongate, various sacs 693 × 209 μm, 781 × 242 μm, 860 × 220 μm (as in figure), and 1,023 × 231 μm, average dimensions 839 × 226 μm; containing many small eggs with diameter 47-57 μm.

Rostrum (Fig. 7a).—Broad with weakly sclerotized rounded posteroventral margin.

First antenna (Fig. 7b).—Six-segmented, 320 μm long. Lengths of segments (measured along their posterior nonsetiferous margins): 29 (49 μm along anterior margin), 88, 55, 26, 36, and 52 μm, respectively. Armature: 5, 15, 9, 4 + 1 aesthete, 2 + 1 aesthete, and 7 + 1 aesthete. All setae smooth.

Second antenna (Fig. 7c).—Four-segmented. First segment with distal seta. Second segment with distal seta and crescentic row of small spines. Third segment with outer marginal row of spines and 2 large recurved clawlike spines, 34 and 70 μm. Small fourth segment 13 × 21 μm, bearing 3 long recurved almost clawlike setae and 1 smaller inner seta.

Labrum (Fig. 7d).—Posteroventral edge sharply pointed medially. No surface ornamentation.

Mandible (Fig. 7e).—Elongate with distal end bearing 2 helmet-shaped elements and 1 stout pectinate spine.

Paragnath (Fig. 7f).—Small lobe with few distal spinules.

First maxilla (Fig. 7g).—Small lobe bearing 5 setae.

Second maxilla (Fig. 7h).—Two-segmented. Large first segment with patch of outer spinules (Fig. 7j). Second segment clawlike and bearing 1 seta.

Maxilliped (Fig. 7i).—Reduced to 2 small setae, located as in Figure 7j.

Legs 1-4 (Figs. 7k, 8a, b, c).—Intercoxal plates with 2 groups of spines on distal (ventral) margin. Exopods and endopods 3-segmented. Armature as follows (Roman numerals indicating spines, Arabic numerals representing setae):

P_1	coxa	0-0	basis	1-I	exp	I-0;	I-1;	III,5
					enp	0-1;	0-1;	I,5
P_2	coxa	0-0	basis	1-0	exp	I-0;	I-1;	III,6
					enp	0-1;	0-2;	III,3
P_3	coxa	0-0	basis	1-0	exp	I-0;	I-1;	III,6
					enp	0-1;	0-2;	III,3
P_4	coxa	0-0	basis	1-0	exp	I-0;	I-1;	III,5
					enp	0-1;	0-1;	III,2

Leg 1 (Fig. 7k).—Coxa with 2 groups of outer spines. Basis with row of small spines between bases of rami and another row near large inner spine. This inner spine delicately barbed (Fig. 7l) and 33 μm long; smaller spines near its base 7.5 μm. First segment of endopod with outer margin having hairlike setules along proximal half but small spines along distal half.

Leg 2 (Fig. 8a).—Basis without inner spine. First segment of endopod with hairlike setules along outer margin.

Leg 3 (Fig. 8b).—Fine ornamentation resembling that of leg 2.

Leg 4 (Fig. 8c).—Coxa with only 1 group of outer spines.

Leg 5 (Fig. 8d).—Two-segmented. First segment 130 × 125 μm, with distal outer seta and group of spines. Second segment elongate, 161 × 68 μm, with 2 outer smooth spines, 52 and 55 μm, distal smooth seta 70 μm, and terminal finely barbed spine 147 μm. These 3 spines with small spines near their insertions. Two groups of small spines on inner side of segment.

Leg 6 (Fig. 6i).—Probably represented by 2 setae on genital area.

Color.—Living specimens in transmitted light with opaque gray body, eye red.

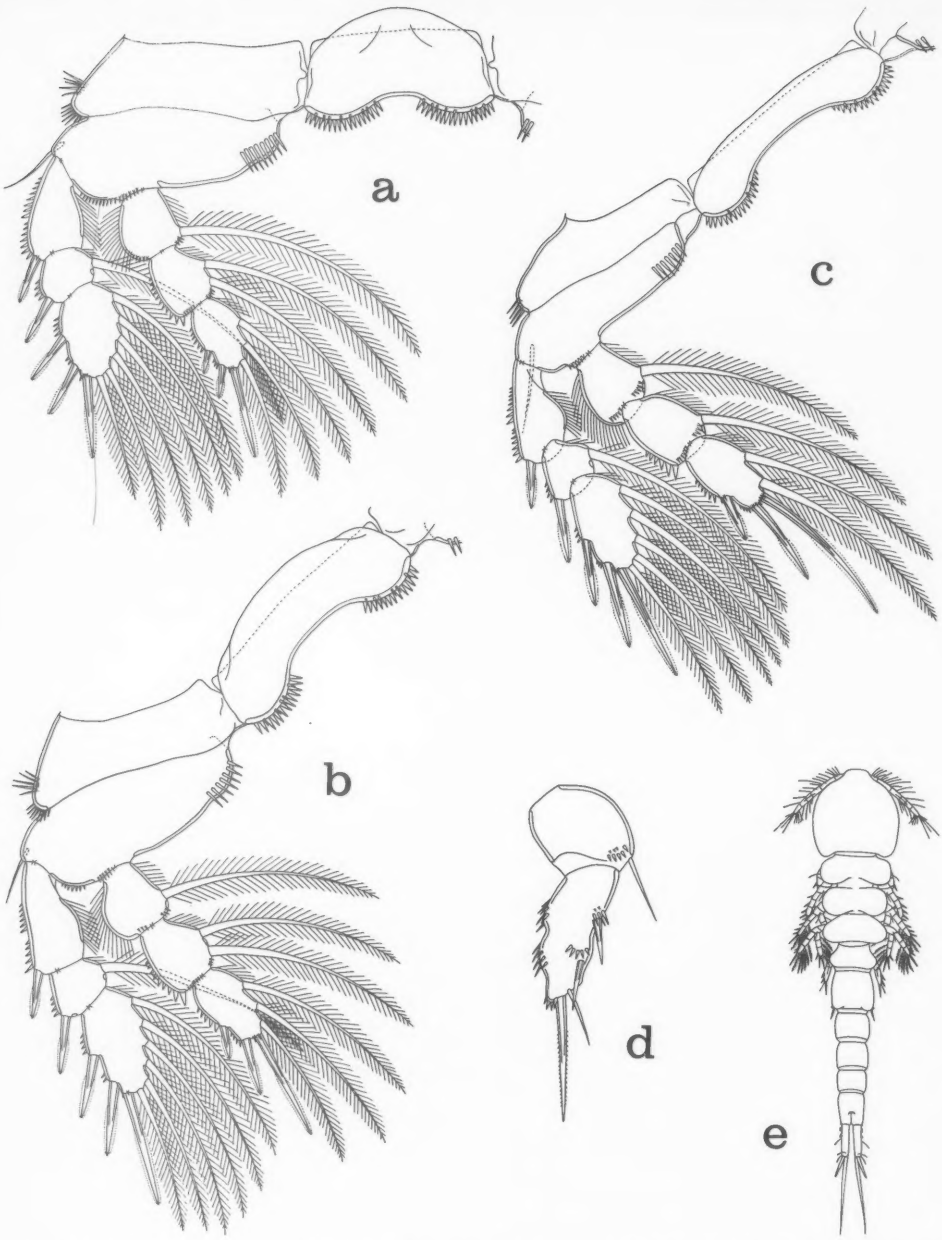

FIGURE 8.—Adult female of *Leptinogaster major*, a-d: a, leg 2 and intercoxal plate, anterior (scale F); b, leg 3 and intercoxal plate, anterior (F); c, leg 4 and intercoxal plate, anterior (F); d, leg 5, lateral (A). Adult male of *Leptinogaster major*: e, dorsal (I).

Adult Male

Figures 8e, 9a-j

Size.—Length 1.82 mm (1.70-2.04 mm) and greatest width 0.43 mm (0.40-0.47 mm), based on 10 specimens.

Body form (Fig. 8e).—Similar to female but 10 body segments including and posterior to segment of leg 1. Urosome (Fig. 9a) 6-segmented. Segment of leg 5 135 × 236 μm in dorsal view, with spines on ventral surface as in female. Four postgenital segments from anterior to posterior 140 × 166, 135 × 143, 113 × 128, and 151 × 109 μm. Anal segment with spines as in female. Cephalosome ventrally with outer strip of small spines and small sclerotized area as in female.

Caudal ramus (Fig. 9a).—As in female but dimensions 174 × 38 μm, ratio 4.6:1.

Rostrum, first antenna, second antenna, labrum, mandible, paragnath, first maxilla, and second maxilla as in female.

Maxilliped (Fig. 9b).—Four-segmented. First segment with 1 inner smooth seta 50 μm. Elongate second segment with 2 inner setae and 2 groups of short spines. Small third segment unarmed. Claw 208 μm, proximal part representing fourth segment bearing 3 setae. Concave margin of claw striated.

Legs 1-4.—With segmentation and armature as in female, and ornamentation as in that sex except for endopod of leg 2.

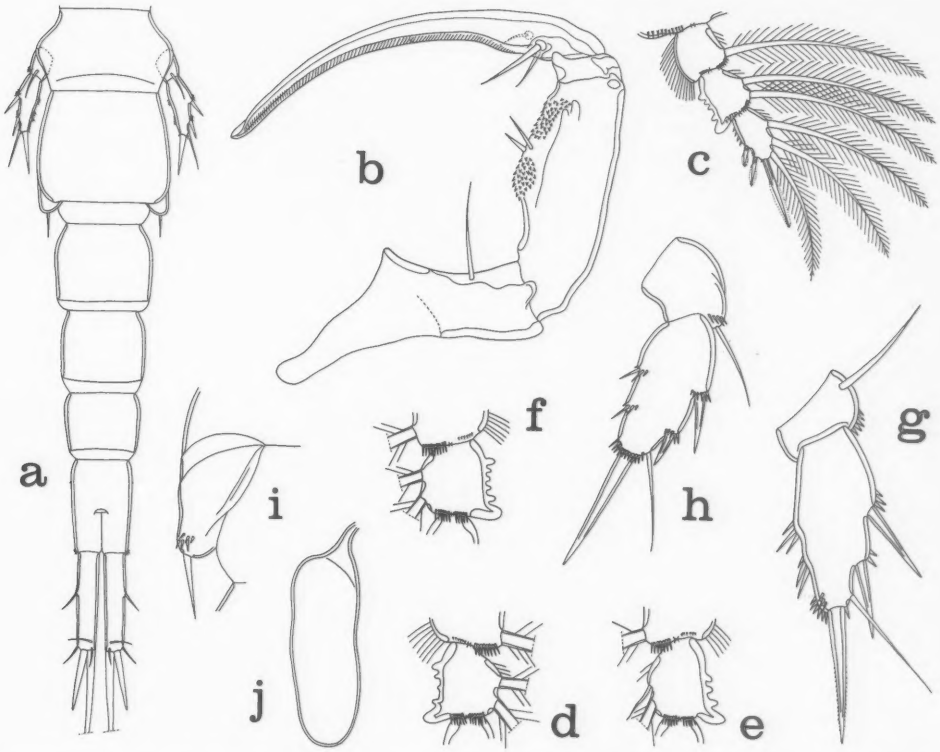

FIGURE 9.—Adult male of *Leptinogaster major*: a, urosome, dorsal (scale H); b, maxilliped, posterior (B); c, endopod of leg 2, anterior (F); d, second segment of endopod of right leg, anterior (B); e, second segment of endopod of left leg (same individual as in d), anterior (B); f, second segment of endopod of leg 2, anterior (B); g, leg 5, dorsal (B); h, leg 5, ventrolateral (B); i, leg 6, ventral (F); j, spermatophore, attached to female, ventral (A).

Leg 2 (Fig. 9c).—Endopod showing sexual dimorphism in having variable nodose outer margin on second segment (Fig. 9d, e, f). Number of nodes from 4-6, and not always same in 1 individual, as in Fig. 9d, e.

Leg 5 (Fig. 9g, h).—Resembling that of female. Second segment in 2 individuals 101 × 47 μm (Fig. 9g) with 4 major elements from proximal to distal 45, 42, 80, and 78 μm, and 86 × 42 μm (Fig. 9h) with elements 22, 26, 65, and 73 μm.

Leg 6 (Fig. 9i).—Represented by single smooth seta 49 μm and adjacent group of small spines on corner of genital area.

Spermatophore (Fig. 9j).—Elongate, approximately 220 × 78 μm without neck.

Color.—As in female.

DISCUSSION

This study permits certain observations to made concerning the postnaupliar development of *Leptinogaster major*. A summary of these is given in Table 3.

1) All five copepodid stages are present in the mantle cavity of *Mya arenaria*.

2) The presence of Copepodid I in *Mya* suggests that either the last nauplius molts outside the clam and then enters, or that this nauplius enters the clam and then molts.

3) Copepodid I is *Saphirella*-like in body form; Copepodid II and later copepodids have a body form more like the adult.

4) The number of body segments increases from 5 in Copepodid I to 9 in the adult female and 10 in the adult male.

5) The armature of the caudal ramus remains unchanged from Copepodid I onward, but the caudal ramus lengthens in successive copepodid stages and in the adults.

6) The first antenna is slow in reaching final form, being 5-segmented in Copepodid I and not reaching its fully 6-segmented condition until the adult.

7) The second antenna has an indistinct fourth segment in Copepodid I, but is clearly 4-segmented thereafter.

8) The labrum of Copepodid I is broad and ornamented with spines, but in Copepodid II and subsequently it is pointed and smooth.

9) The mandible of Copepodid I is a simple blade, but in Copepodid II and succeeding stages there are 3 terminal elements as in the adult.

10) The first maxilla of Copepodid I is similar to that of Copepodid II and following stages.

11) The second maxilla has terminal setae in Copepodid I but a terminal claw thereafter.

12) The maxilliped in Copepodid I is elongate and 4-segmented with long setae, but in Copepodid II and Copepodid III it is small with 4 weak unarmed segments. From this point on, the maxilliped in the female shows further reduction, while in the male it undergoes enlargement and specialization. In the female of Copepodid IV it is minute, 2-segmented, and unarmed; in Copepodid V and in the adult it is reduced to 2 small setae. In the male of Copepodid IV the maxilliped is 3-segmented, pointed, with 2 setae; in Copepodid V it is 4-segmented, pointed, with 3 setae; in the adult male it is 4-segmented with a long terminal claw.

13) The full complement of 4 biramous 3-segmented legs is not reached until Copepodid V.

14) The inner spine on the basis of the endopod of leg 1 first appears in Copepodid II.

15) Leg 5 is absent in Copepodid I and Copepodid II, is represented by 2 setae in Copepodid III, and abruptly becomes 2-segmented with full armature in Copepodid IV.

16) Sexual dimorphism in legs 1-4 occurs only in the endopod of leg 2 in the adult male.

17) Sexual differentiation during copepodid development first occurs in Copepodid IV, where the male and female maxillipeds are differently formed.

The maxilliped in the adult female is said to be absent in *Leptinogaster histrio* (Bocquet and Stock 1958; Băcescu and Por 1959), in the genus *Myocheres* (Wilson 1950), in *Leptinogaster inflata* (Allen 1956), in *Leptinogaster scobina* (Humes and Cressey 1958), and in *Leptinogaster dentata* (Humes and Cressey 1958). The maxilliped has now been traced throughout copepodid development, and it is apparent that a remnant of this appendage exists in the adult female of *L. major*.

This discovery prompted a reexamination of adult females of two species of *Leptinogaster*, *L. scobina* and *L. dentata*. In both the maxilliped is represented by two very small setae, as in *L. major*. It is not surprising that these setae were overlooked, since they are very minute and readily seen only in well-cleared specimens.

Although the remaining species of *Leptinogaster*, *L. histrio* (Pelseneer, 1929), *L. pholadis* (Pelseneer, 1929), *L. inflata* (Allen, 1956), and a new species con-

TABLE 3.—Comparison of selected external features during copepodid stag

	Copepodid I	Copepodid II	Copepodid III	Copepodid IV ♀	Copepodid IV ♂
No. of body segments	5	6	7	8	8
First antenna	5-segmented	5-segmented	5-segmented	5-segmented	5-segmented
Second antenna	indistinctly 4-segmented	4-segmented	4-segmented	4-segmented	4-segmented
Labrum	broad, spined	pointed, smooth	pointed, smooth	pointed, smooth	pointed, smooth
Mandible	simple blade	3 terminal elements	3 terminal elements	3 terminal elements	3 terminal elements
Second maxilla	terminal setae	terminal claw	terminal claw	terminal claw	terminal claw
Maxilliped	slender, 4-segmented, long setae	small, 4 weak unarmed segments	small, 4 weak unarmed segments	minute, 2 weak unarmed segments	3-segmented, pointed, 2 setae
Rami of leg 1	1-segmented	2-segmented	2-segmented	2-segmented	2-segmented
Rami of leg 2	1-segmented	2-segmented	2-segmented	2-segmented	2-segmented
Rami of leg 3	2 setae only	1-segmented	2-segmented	2-segmented	2-segmented
Rami of leg 4	absent	2 setae	1-segmented	2-segmented	2-segmented
Leg 5	absent	absent	2 setae	2-segmented	2-segmented
Leg 6	absent	absent	absent	1 seta	1 seta

d stages and adults of *Leptinogaster major.*

id IV	Copepodid V ♀	Copepodid V ♂	Adult ♀	Adult ♂
	9	9	9	10
nted	incompletely 6-segmented	incompletely 6-segmented	6-segmented	6-segmented
nted	4-segmented	4-segmented	4-segmented	4-segmented
	pointed, smooth	pointed, smooth	pointed, smooth	pointed smooth
al nts	3 terminal elements	3 terminal elements	3 terminal elements	3 terminal elements
claw	terminal claw	terminal claw	terminal claw	terminal claw
nted, d, e	2 setae on slight lobe	4-segmented, pointed, 3 setae	2 setae	4-segmented, long terminal claw
nted	3-segmented	3-segmented	3-segmented	3-segmented
nted	3-segmented	3-segmented	3 segmented	3 segmented, sexual dimorphism in endopod
nted	3-segmented	3-segmented	3-segmented	3-segmented
nted	2-segmented	3-segmented	3-segmented	3-segmented
nted	2-segmented	2-segmented	2-segmented	2-segmented
	1 seta	1 seta	2 setae on genital area	1 seta

tained in Gooding's thesis (1963) have not been reexamined, it appears likely that the presence of a very reduced maxilliped in the adult female is a generic character in *Leptinogaster*.

Gooding (1963:218-220) discussed the generic status of *Saphirella* T. Scott, 1894, pointing out that species of *Saphirella* may represent Copepodid I stages of clausidiids. In his thorough description of Copepodid I of *Leptinogaster* a significant difference seems to be in the body length, which Gooding gave as 0.45 mm, while in this study the length is 0.57 mm (0.45-0.60 mm).

Although the genus *Leptinogaster* has been assigned to various families (Table 1), its presently agreed location appears to be in the Clausidiidae Embleton, 1901, along with *Clausidium* Kossmann, 1874, *Conchyliurus* Bocquet and Stock, 1957a, *Giardella* Canu, 1888, *Hemicyclops* Boeck, 1873, *Hersiliodes* Canu, 1888, and *Hippomolgus* G.O. Sars, 1917. [According to the phylogenetic analysis of Ho (1984), the genus *Myzomolgus* Bocquet and Stock, 1957b, should be removed from the Clausidiidae and placed close to the Catiniidae Bocquet and Stock, 1957b.] The family Clausidiidae, containing seven genera of certain status, shows several features: first antenna 6- or 7-segmented; second antenna 4-segmented with third segment having in some cases prehensile elements and fourth segment without a strong claw; mandible with spine (or spinelike process) and 2 or 3 accessory elements (setae, spines); labrum with rounded margin, mostly entire without median indentation, except triangular in *Leptinogaster*; first maxilla often with 2 lobes, but with 1 lobe having 2 groups of setae in *Leptinogaster* and 1 lobe with a few setae in *Clausidium*; maxilliped in female mostly 2-, 3-, or 4-segmented, but in *Leptinogaster* reduced to 2 setae; maxilliped in male 2- or 3-segmented plus claw (in *Hippomolgus* male unknown); legs 1-4 biramous and 3-segmented (endopod of leg 1 bearing suckers in *Clausidium*); leg 5 2-segmented (though in some first segment not clearly separated from body).

Leptinogaster falls within this concept of the family Clausidiidae. Neighboring families have fundamentally different features, e.g., the Clausiidae (first antenna 3-6 segmented; legs 1-4 showing various degrees of reduction (as characterized by Wilson and Illg (1955)), the Myicolidae (3-segmented second antenna with strong terminal claw, maxilliped in female a small unarmed lobe), and the Ergasilidae (second antenna with a strong terminal claw, maxilliped often absent in female, legs 1-4 with some reduction). More information on the developmental stages of the members of these families would contribute greatly to understanding their interrelationships.

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REPRODUCTIVE BIOLOGY OF FEMALE SPOTTED DOLPHINS, *STENELLA ATTENUATA*, FROM THE EASTERN TROPICAL PACIFIC

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ABSTRACT

Reproductive parameters were estimated from about 4,700 female spotted dolphins collected in the eastern tropical Pacific from 1973 to 1981. From this sample, specimens for which ages were estimated were divided into two subsets and were used to estimate age-specific rates for the northern offshore stock of this species. The youngest sexually mature individual was 10 years old; the oldest immature was 17 years; the youngest and oldest pregnant individuals were 10 and 35 years, respectively. There was high individual variability in the accumulation of corpora with age; the ovulation rate appears to slow abruptly after the eighth ovulation. Average age at attainment of sexual maturity (ASM) for all years ranged from 10.7 to 12.2 years ($\bar{x}$ = 11.4 years) for two sets of age estimates; no significant temporal change in ASM was detected. Correlation between color phase and state of sexual maturity suggests that color phase may be a good indicator of maturity for this stock. The average annual pregnancy rate was about 0.33; this rate did not change significantly with age. The calving interval was 3.03 years (SE = 0.205). The lactation period was 1.66 years, but there was a significant increase noted in the percent lactating from 1973 to 1981. A low percentage of postreproductive females was found in the sample (0.4%) indicating that reproductive senescence is of little importance in reproductive rates of this stock.

Purse seine operations of the yellowfin tuna fishery in the eastern tropical Pacific Ocean (ETP) have caused high mortality of the spotted dolphin, *Stenella attenuata* (Perrin 1969a, 1970). Estimated incidental kills for the northern offshore stock of spotted dolphins were between 100,000 and 400,000 annually throughout the 1960's and early 1970's (Smith 1983). Since 1968, research efforts by the National Marine Fisheries Service (NMFS) have focused on assessing the biological consequences of the large incidental kill of this and other affected dolphins using specimens and data collected by NMFS observers aboard U.S. tuna seiners. Perrin et al. (1976) presented the first comprehensive description of spotted dolphin life history and reproduction for specimens from the ETP. The accumulation of thousands of additional specimens, the sharp decline in dolphin mortality (Smith 1983; Hammond and Tsai 1983), and the improvements made in estimating age since that study (Myrick et al. 1983) have made a new analysis necessary.

The purpose of this paper is to estimate the reproductive parameters of the female spotted dolphin, based on analyses which include more data and a better age estimating method than previous studies. Reproductive features of the male spotted dolphin (Hohn et al. 1985) and temporal trends in reproduction in the northern offshore stock (Barlow 1985) are discussed in separate papers.

MATERIALS AND METHODS

Samples

The specimens were analyzed as three samples. The "overall" sample contained about 4,700 specimens that had been collected from 1973 through 1981. A second sample for which ages were estimated contained 580 specimens selected randomly from more than 3,500 specimens collected in 1973 through most of 1978 (the 1973-78 aged sample). The randomly chosen 1973-78 aged sample did not include any of the specimens studied by Perrin et al. (1976). The third sample (the 1981 aged sample) was composed of 226 specimens which had been collected in 1981 and for which ages were estimated. It included almost all specimens for which ovaries and teeth were collected in that year. The two aged samples, referred to collectively as the aged sample, are subsets of the overall sample. In several analyses the 1973-78 aged sample was divided into 1973-74 and 1975-78 subsamples in an effort to detect possible temporal changes in reproductive rates. Only the

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northern offshore stock of spotted dolphins (as defined by Smith 1983) is treated in this analysis. The geographic boundary used to divide it from a southern stock is lat. 1°S (Henderson et al. 1980).

Life History Data

Data and specimens were collected by biological technicians aboard tuna purse seine vessels in the ETP. Biological data used in this analysis are body length, color phase, reproductive condition (pregnant, lactating, or resting), and corpora counts for each specimen (see Perrin et al. [1976] for a description of collection and examination procedures). Although there is no certainty that all ovarian corpora persist for life in all delphinids (Perrin and Reilly 1984), corpora counts were used with age to estimate ovulation rates. Counts included corpora albicantia (CAs), corpora lutea (CLs), and in some cases corpora atretica (atretic follicles). Only specimens that had both ovaries examined were included in the ovulation rate analyses.

Age Estimates

Ages were estimated for about 800 specimens (from 1973 to 1978 and 1981 samples) by counting growth layer groups (GLGs, Perrin and Myrick 1980) in the dentine and cementum of decalcified and hematoxylin-stained thin sections (Myrick et al. 1983). Tooth readings were made independently by two readers (A. C. Myrick and A. A. Hohn), without referring to field or laboratory data on size or reproductive condition. For the 1973-78 sample, a tooth of each specimen was read at least three times by each reader. Age estimates by each reader were significantly different (Reilly et al. 1983). To minimize the differences, the mean of the multiple age estimates by each reader was calculated and the average of the two means was used as the estimate of a specimen's age. For the 1981 sample a tooth from each specimen was read once by each reader after calibration tests showed that differences in estimates between readers were acceptably small (Reilly et al. 1983). An average of these two readings was used for specimen age.

We consider the method we used to estimate ages improved over that used by Perrin et al. (1976) because

1) the preparation technique we used provides superior resolution of GLGs (Myrick et al. 1983);

2) the new method of reading utilizes GLGs in the cementum as well as in dentine and allows a more accurate estimate of maximum age for adults (Myrick et al. 1983; see also Kasuya 1976);

3) calibration of GLGs in tetracycline-labeled teeth of Hawaiian spinner dolphins, *Stenella longirostris* (Myrick et al. 1984), has provided a basis for interpreting dental layering within an absolute-time framework (Myrick et al. 1983; Myrick et al. 1984). Perrin et al. (1976) used the term tooth layers in lieu of known time units.

RESULTS AND DISCUSSION

Composition of Samples

Chi-square (contingency) tests were used to evaluate whether fractions of mature, pregnant, and lactating females in the 1973-78 aged sample were a representative subset of the overall sample for those years. For all three tests, differences were not significant ($P > 0.05$).

Reproductive statistics showed some differences between years (Table 1). Chi-square tests were carried out for homogeneity between 1973-74 and

TABLE 1.—Number of sexually mature, pregnant only, lactating only, simultaneously pregnant and lactating, and "resting" female spotted dolphins, and the proportion of the sample pregnant or lactating in the aged and overall samples. The proportion pregnant and proportion lactating include the simultaneously pregnant and lactating specimens.

	Number					Proportion	
Years	Sexually mature	Pregnant only	Lactating only	Pregnant and lacting	Resting	Pregnant	Lactating
Aged							
1973-74	188	57	87	7	38	0.34	0.50
1975-78	205	48	100	13	44	0.30	0.55
1981	149	34	86	9	17	0.29	0.64
Total	542	139	273	29	99	0.31	0.56
Aged and unaged							
1973-81	2,979	780	1,480	151	568	0.31	0.55

1981 aged samples and between 1975-78 and 1981 aged samples for numbers of specimens pregnant, lactating, and resting. These tests revealed significant differences (1973-74 vs. 1981: $\chi^2_2 = 7.46$, $P = 0.024$; 75-78 vs. 1981: $\chi^2_2 = 6.16$, $P = 0.046$.). These differences are the result of an increase in the relative frequency of lactating females (see section on Lactation Period). There were no differences in percent pregnant during this time (see also Barlow 1985).

Ovulation Rate

Individual Variability

Perrin et al. (1976) found high variability in the number of corpora (corpora atretica included) for a given age (in tooth layers). Nevertheless, by fitting a power curve to the average number of corpora as a function of average reproductive age, they determined that the average ovulation rate slowed abruptly from about "four during the first layer, [to] two during the second, and about one per layer thereafter" (Perrin et al. 1976, p. 261).

The sexually mature specimens in the combined aged samples were used in our study to plot average frequency of corpora (corpora atretica excluded) on estimated age (Fig. 1). Regressions for the 1973-74 sample and for the 1981 sample are not significantly different; when the samples are pooled, the resulting slope is 0.61 corpora/yr. A plot of number of corpora on age for all individuals ($n = 542$) in mature age classes (10 through 38 yr old) for all aged specimens (Fig. 2) showed a significant slope ($P < 0.0001$) but a low correlation ($r^2 = 0.397$), indicating high individual variability. For example, the sample included 12- and 13-yr-olds with 7 or 8 corpora, and 21-yr-olds with 4 or fewer corpora. A 38-yr-old had only 11 corpora (Table 2). These results support those of Sergeant (1962), Brodie (1971), Kasuya et al. (1974), and Perrin et al. (1976), that great individual variation occurs in ovulation rates among odontocetes.

TABLE 2.—Summary of age-related reproductive statistics for female spotted dolphins taken in 1973-78 and 1981.

Variable	Estimated age (years)
Range of ages with no corpora	0-17
Oldest with one corpus	23
Youngest with one corpus	10
Youngest pregnant	10
Oldest pregnant	35
Average age pregnant	18
Oldest simultaneously pregnant and lactating	29
Oldest lactating	36
Youngest lactating	10
Oldest	38

Changes in Rate

Ovulation rate apparently decreases with reproductive age. If ovulation and mortality rates were

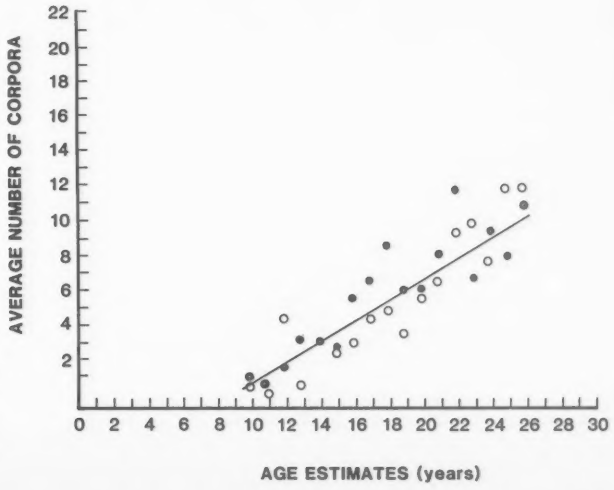

FIGURE 1.—Linear regression of number of corpora on estimated age as gross estimates of ovulation rates in female spotted dolphins. Points represent averages for 1-yr age classes (1973-78 samples = closed circles; 1981 sample = open circles).

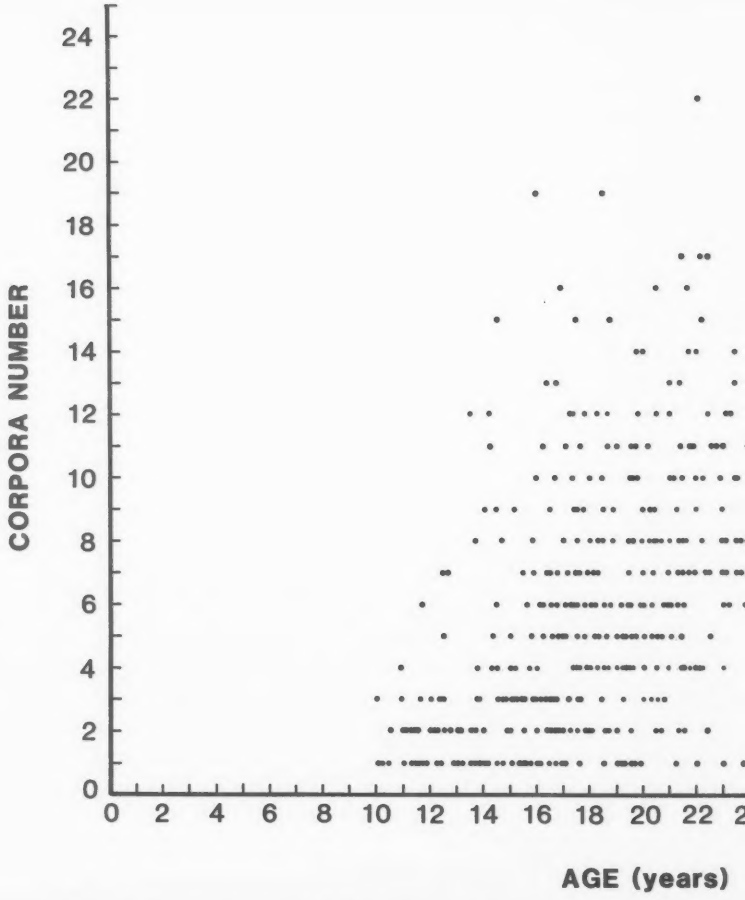

FIGURE 2.—Plot of total corpora (excluding corpora atretica) on estimated age for 542 mature f

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ature female spotted dolphins collected in 1973-78 and 1981.

constant, a semilog plot of the frequency distribution of corpora counts would be linear. The slope of this line would be negative, and its value would be determined by mortality and ovulation rates. The observed shape of the log-frequency distribution of corpora counts for spotted dolphins (Fig. 3) suggests that ovulation and/or mortality rates are not constant. After about eight ovulations, log-frequencies decrease monotonically and nearly linearly. For up to the first eight ovulations, the rate is apparently much higher (presuming, again, that mortality rates do not change with the number of ovulations and that all CAs persist for life [Perrin and Reilly 1984]). This supports the findings of Perrin et al. (1976) that ovulation rates decrease with reproductive age in spotted dolphins.

Sexual Maturity

The age at which a female first ovulates is considered the age at attainment of sexual maturity (DeMaster 1978, 1984). Using the aged samples, we estimated average age at sexual maturity (ASM) using two methods. For these estimates, ages were grouped by 1-yr intervals: age-class 1 included specimens 0-1.0 yr, age-class 2 from 1.1 to 2.0 yr, etc. The mean age of sexually mature females was 18.7 yr.

Method-One

ASM was estimated from both readers' age estimates using a variation of the method described by DeMaster (1978). Age-specific maturation rates were used to calculate mean ASM as

$$\text{ASM} = \sum_{x=1}^{w} (x - 0.5)\, P_x$$

where x is age class, P_x is the probability of first ovulating in age class x, and w is the maximum age in the sample. The term $(x - 0.5)$ was substituted for DeMaster's (x) so that the mean age in an age-class interval would be represented by the midpoint of that interval. The terms P_x were estimated as

$$P_x = f(x + 1) - f(x),$$

where $f(x)$ is the probability of being mature at age x. The function $f(x)$ was estimated as the best least-squares fit of a curve (York 1983) to the observed values of percent mature by age class. A 3-parameter sigmoid curve based on a modification of the logistic equation was found to give an adequate fit of the data (Fig. 4).

ASMs were calculated separately for the aged samples, 1973-74, 1975-78, and 1981. There were no significant differences among these samples ($P > 0.05$). The ASM for all samples combined was 10.7 (var. = 0.03) to 12.2 (var. = 0.05) yr for the two readers. The average of these two ASM estimates was 11.4 yr. The precision between readers in age estimates of the 1981 specimens was greater than

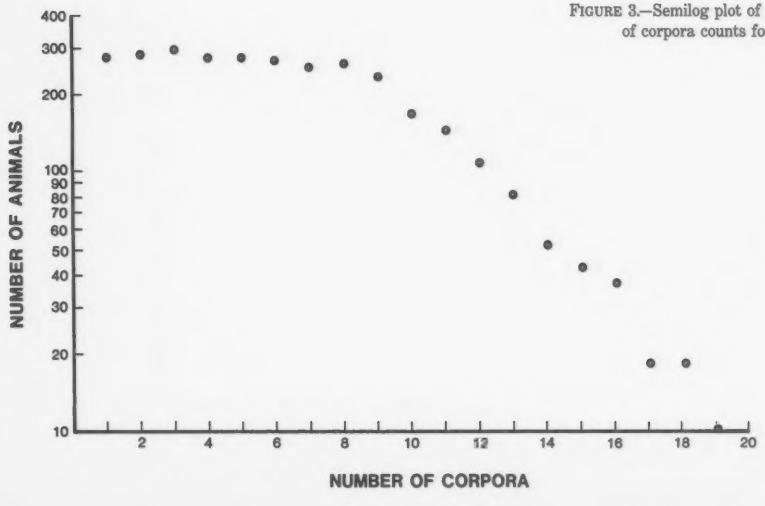

FIGURE 3.—Semilog plot of the frequency distribution of corpora counts for female spotted dolphins.

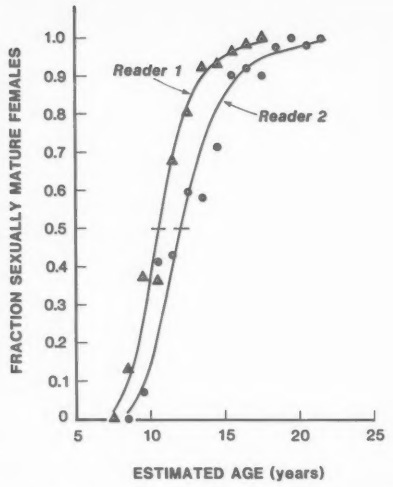

FIGURE 4.—Fraction of sexually mature female spotted dolphins versus age based on estimates of two readers. Logistic curves are fitted to the data. Bars predict ages at which 50% are sexually mature.

for the 1973-78 specimens (Reilley et al. 1983); the mean ASM range for the 1981 sample was 11.6-11.7 yr.

Method Two

The second method we used for estimating ASM was to interpolate, from a maturation curve, the age at which 50% of the specimens were mature. Again, sigmoid curve fits of the percent of mature specimens as a function of age were used for the maturation curves. For all aged samples combined, the method predicts an ASM of 10.6-12.0 yr (for the two readers), with an average of 11.3 yr.

Our overall estimates of ASM (11.3 or 11.4 yr) differ markedly from the ASM estimated for ETP spotted dolphins by Perrin et al. (1976) which was 9 tooth layers, "5.1 to 8.3 yr, depending on [which] layering hypothesis is used" (p. 250). Our estimates also differ from the ASM estimate for spotted dolphins off the Japanese coast by Kasuya (1976) which was 9 yr.

Biases in ASM

All of the above estimates of ASM are dependent on two important assumptions. First, we assume that counts of dentinal and cemental GLGs give precise and unbiased estimates of age. Second, we assume that our samples are unbiased with respect to the maturity of the specimens collected. Potential biases would result if the assumptions were invalid. Because age estimates of the two readers differ significantly (Reilly et al. 1983), the difference in ASM estimates for the readers (1.5 yr) should be taken as a minimum range in the ASM estimates.

Color Pattern and Maturity

Perrin (1969b) described the ontogenetic development of color pattern in spotted dolphins in the ETP: he divided the development into five sequential phases (neonatal, two-tone, speckled, mottled, and fused) based on patterns of ventral and dorsal spots. Kasuya et al. (1974) described color-phase changes in western Pacific spotted dolphins using somewhat different definitions than those of Perrin (1969b), although the description indicated that the ontogenetic changes were similar to those observed by Perrin. Perrin (1969b) found a close correlation between size and color pattern and (for a smaller sample) between sexual maturity and color pattern. Kasuya et al. (1974) found that the development of the adult color pattern in spotted dolphins from the western Pacific coincides with the attainment of sexual maturity.

In our sample of spotted dolphins, there was considerable overlap in age and length between animals with different color patterns, but a correlation between color pattern and state of maturity was evident. In females from the aged sample, speckled animals ranged from 3 to 18 yr, mottled from 6 to 32 yr, and fused from 10 to 38 yr. A similar overlap occurred in body-length distribution from the overall sample of females, 135-200 cm (n = 166), 140-210 cm (n = 179), and 155-220 cm (n = 188) for speckled, mottled, and fused specimens, respectively. However, 96% of fused animals (n = 2,764), 50% of mottled animals (n = 857), and only 4% of speckled animals (n = 559) were sexually mature.

In addition, for a given length or age class, females with a fused color pattern appeared to have been mature for a longer time than animals with a mottled pattern. For females of similar lengths, mature specimens with a fused color pattern had more corpora than those with a mottled color pattern (Fig. 5). Similarly for the aged sample, the fused specimens within a given length group tended to have more total corpora than mottled specimens, and when specimens in the same body length categories were of similar ages, fused animals had more total corpora.

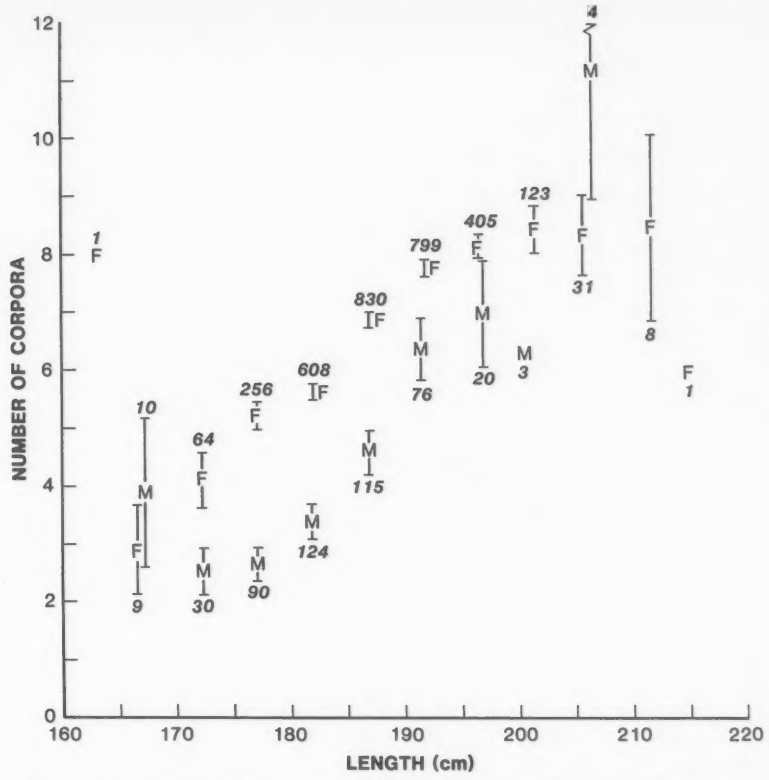

FIGURE 5.—Average number of corpora for mottled (M) and fused (F) color-phase specimens within each 5 cm length grouping for the overall sample of female spotted dolphins. Bars represent one standard error from the mean. Sample sizes are shown.

These results suggest that color phase may indicate sexual maturity more accurately than either age or length. Perrin (1969b) found 0% speckled (n = 5), 60% mottled (n = 16), and 100% fused (n = 33) females to be sexually mature. Using color phases that roughly correspond to the late mottled and fused stages of Perrin (1969b), Kasuya et al. (1974) found that 93% (n = 30) of the spotted dolphins in the third stage and 100% in the last (fourth) stage of dorsal spotting were sexually mature. A similar relationship between maturity and color pattern exists in male spotted dolphins in the ETP (Hohn et al. 1985). Assuming that the proportion of mature specimens in a given color phase does not change within a population, it would be possible to estimate the percentage of sexually mature specimens in a sample without having to examine the ovaries for corpora.

Pregnancy Rate

The annual pregnancy rate (APR) of a population is the fraction of mature females that would be expected to give birth in any given year. APR can be estimated as the average fraction of mature females that are pregnant divided by the gestation time in years. The variance of this estimate is approximated by

$$\text{var(APR)} = (-P/T_G^2)^2 \text{ var } (T_G) + (1/T_G^2)\, P(1 - P)/n_p$$

where P is the proportion pregnant, T_G is the gestation time, and n_p is the sample size used to estimate P (Perrin and Reilly 1984). We use 0.958 yr (11.5 mo) as the gestation period for spotted

dolphins (Perrin et al. 1976). The variance in gestation time has not been calculated. We can, however, reasonably estimate that 95% confidence limits would span 0.1 yr. From this we estimate the var (T_G) to be 0.000625.

For the aged sample, 31.1% of the sexually mature specimens (n = 542) were pregnant. For the overall sample during the same years, 31.6% of the sexually mature specimens (n = 2,458) were pregnant and for all aged and unaged mature specimens from 1973 through 1981 inclusive (n = 2,979), 31.3% were pregnant (Table 1). By dividing the fraction of pregnant females by the gestation period (0.958), annual pregnancy rates of 0.325 and 0.330 were obtained for the aged and overall samples, respectively. The var(APR) for the overall sample is 0.0005.

To determine whether pregnancy rates changed with age, we estimated percent pregnant for four age-class intervals using the 1973-78 and 1981 samples combined. Sample size was small for estimating age-specific rates with much precision. Nevertheless, we detected neither a sustained increase nor a sustained decrease in the percent of pregnant females with age (Fig. 6); the variability in the percent of pregnant females with age can be accounted for by random sampling (χ^2_3 = 4.6, $P >$ 0.50). This result differs from that of Perrin et al. (1976) which indicated a significant reduction in pregnancy rate with age.

Calving Interval

Calving interval is an estimate of the mean period between births for mature females. Typically, it is estimated as the inverse of the annual pregnancy rate (Perrin and Reilly 1984). The principal requirements for calculating the calving interval are unbiased estimates of gestation time and of the fraction of mature females that are pregnant. The standard error in an estimate of calving interval (CI) by these methods is approximated by

$$\text{SE (CI)} = \text{(APR-4) var(APR)}$$

(Perrin and Reilly 1984).

Given our calculated APR estimate of 0.330 for the overall sample, the calving interval is 3.03 yr. The standard error of this estimate is about 0.205. Although it is difficult to prove that our estimates of the percent of pregnant females are unbiased, support for such a position is given by Barlow's finding that the percent of pregnant females varies little with sampling conditions (including sampling season, geographic area, dolphin school size, and dolphin killer-set) (Barlow 1985). However, if annual variability in the percent of pregnant females is important, binomial sampling theory is likely to underestimate our certainty in estimating the percent of pregnant females, APR, and calving interval. Because no significant trends were detected in the percentage

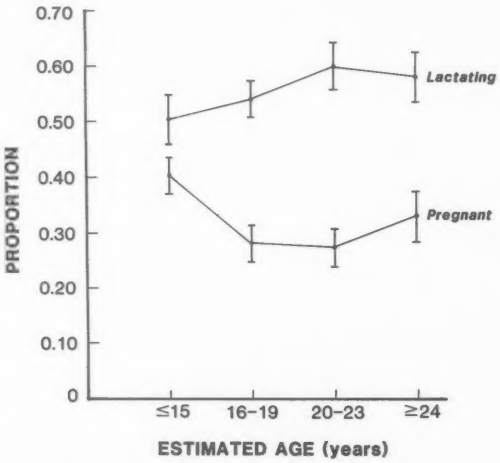

FIGURE 6.—Proportion lactating and proportion pregnant as a function of age for sexually mature female spotted dolphins, in 1973-78 and 1981. Bars represent one standard error from the mean (n = 542).

of pregnant females from 1974 to 1983 (Barlow 1985) and because no significant changes were found in pregnancy rates with age, estimates of calving interval were not calculated for any of these possible stratifications.

Previous estimates of calving interval for *S. attenuata* include 2.5 yr for the southern offshore ETP stock, 2.7-3.4 yr for the northern offshore ETP stock, and 3.5-3.9 yr for a western North Pacific population (all values taken from Perrin and Reilly 1984, table 6). Our estimate, 3.06 yr, is thus close to previous estimates for the ETP northern stock and falls between the estimates for two other populations.

Lactation Period

The calving cycle in mammals can be thought of as a gestation period, a lactation period, and (in some cases) a resting period. Since gestation and lactation can overlap, the calving interval can be less than the sum of the gestation and lactation periods.

In this study, the duration of the lactation period was estimated as the fraction of mature females that are lactating multiplied by the calving interval in years. Again, the assumption is that all reproductive stages of mature females are sampled without bias. The estimated lactation period for the overall sample is 1.66 yr.

Unlike the percent pregnant, the percentage of lactating females has apparently increased over the years between 1973-74 and 1981 (Table 1). Collaborative evidence is provided by Barlow (1985). Barlow's weighted regression of the percent of lactating females regressed against year predicts values of 46% lactating for 1971 and 69% for 1983. These correspond to a change in mean lactation period from 1.4 to 2.1 yr.

There were no significant differences in proportion of lactating females in different age-classes for all aged samples combined ($\chi^2_8 = 2.58$, $P > 0.25$) (Fig. 6).

Evidence exists for considerable individual variability in calving interval and lactation period. The sum of the estimated gestation time (0.958 yr) plus the mean lactation period (1.66 yr) is about 2.6 yr; the mean calving interval, estimated as the inverse of APR, is roughly 3 yr. We might predict from this that individuals would never be simultaneously pregnant and lactating. In fact, 16% of the sampled pregnant females were lactating. This is implicit evidence of individual variability.

Postreproductive Females

Several criteria have been used to identify postreproductive female odontocetes. Perrin et al. (1976) described postreproductive spotted dolphins and Perrin et al. (1977) described postreproductive spinner dolphins, *S. longirostris*. Both studies were based on the presence of atrophic ("regressed" or "withered") ovaries. In both cases, the incidence of postreproductive females was 1% or less of the sample. In pilot whales, *Globicephala macrorhynchus*, Marsh and Kasuya (1984) found changes in the histology of the ovary, such as a decrease in the volume of the cortex and sclerosis of the arterial walls that are age related and associated with senescence. Senescent females were characterized on the basis of follicle abundance and the incidence of follicular atresia.

Postreproductive females also occurred in our sample. Nine of the mature females collected from 1973 to 1982 had atrophic ovaries and thus are considered to have been reproductively senescent. Their mean ovary weights and maximum follicle diameters were significantly different from the means of the other mature females collected during these years (t-test, $P < 0.005$) (Table 3, Fig. 7). None was lactating.

Evidence of decreased fertility was found in some females without atrophic ovaries. Two groups were extracted from the aged sample: 1) those specimens that had 20 or more corpora (all but one was 20 yr old or older), and 2) those specimens that were 20 yr old or older and had only four or fewer total corpora (including atretica). Of the first group ($n = 12$), the mean maximum follicle diameter was larger than that of the atrophic-ovary sample (t-test, $P < 0.005$), but the mean weights for both ovaries combined were not significantly different (Table 4). Atretic corpora constituted 24% of the total corpora, less than the frequency of atresia found in the atrophic ovaries (39%). The two specimens in this sample with the highest proportion of corpora atretica also had ovaries with maximum follicle diameter and ovary weights within the range of the atrophic ovaries; in addition, they had no CLs (corpora lutea) or Type 1 corpora. We consider these two females to have been postreproductive. Of the second group ($n = 14$), the mean maximum follicle diameter and ovary weight were not different from those in the sample with more total corpora, but were markedly different from those of the atrophic ovaries (t-test, $P < 0.025$). None of these ovaries contained corpora atretica.

Comparison of females in the two groups provides evidence that when the complement of follicles has nearly been expended (through ovulation or atresia), fertility diminishes. Of the first group, 5 of the 12

TABLE 3.—Combined ovary weights, maximum follicle diameter, and corpora counts in "non-atrophic" (normal) ovaries with no corpus lutem (n = 3,455) and atrophic ovaries (n = 9) of sexually mature female spotted dolphins collected in 1973-82.

Variable	Non-atrophic ovaries		Atrophic ovaries	
	Mean	SE	Mean	SE
Combined ovary weight	4.9	0.05	3.0	0.30
Maximum follicle diameter	2.8	0.06	0.4	0.07
Total corpora excluding atretica	6.8	0.09	12.4	1.36
Total corpora including atretica	7.5	0.11	20.9	1.13
Corpora atretica	0.7	0.04	8.4	1.67
Percent of corpora atretic	6.4	0.30	40.0	7.6

lacked macroscopic follicles. Such specimens have in common: 1) the absence of CLs and Type 1 corpora, 2) a large number of total corpora, 3) a high frequency of atresia (a relatively large proportion of the total corpora), and 4) a maximum follicle diameter of 0.5 mm or less. The incidence of obvious senescence in the sample of spotted dolphins (0.4%) is much less than that in pilot whale samples studied (5% in *Globicephala melaena* from the northern Atlantic Ocean [Sergeant 1962] and 25% in *G. macrorhynchus* from the western Pacific [Marsh and Kasuya 1984]). This may be indicative of inherent differences in the social structure or longevity between pilot whales and spotted dolphins.

TABLE 4.—Mean age, maximum follicle diameter, ovary weight, corpora counts, and reproductive states for female spotted dolphins. Type 1 and Type 2 corpora defined by Perrin et al. (1976).

	Age years	Maximum follicle diameter (mm)	Combined ovary weights (g)	Total corpora[1]	Corpora atretica	Percent atretic	Type 1 corpora	Type 2 corpora	Pregnant/ lactating (%)
A. Females with 20 or more corpora (n = 12)									
Mean	20.2	2.7	4.2	21.3	4.7	21.9	0.5	1.4	40
SE	1.0	0.5	0.5	0.3	0.8	3.6	0.2	0.4	
B. Females 20 yr or older with four or fewer corpora (n = 14)									
Mean	22.6	2.5	5.1	2.7	0	0	0.9	0.9	100
SE	0.5	0.3	0.6	0.3	0	0	0.2	0.2	

[1]Includes atretica.

specimens were pregnant or lactating. All 14 of the second group were pregnant or lactating. Thus, the first group shows reduced fertility when compared with the second group. Marsh and Kasuya (1984) described an age-related decline in follicle abundance in pilot whales, stating that when follicles are "depleted" the animals become senescent. The reduction in fertility indicated in our sample of spotted dolphins is not strictly age-related; it is more dependent on the number of corpora (including corpora atretica) already present in the ovaries. This has been shown to be true in western Pacific spotted dolphins (Kasuya et al. 1974) and in sperm whales (Best 1967).

In addition to the postreproductive females with atrophic ovaries, four mature females with normal-appearing ovaries had no macroscopic follicles (one of the atrophic ovaries contained no macroscopic follicles). This is similar to the condition described by Marsh and Kasuya (1984). The ovaries of these specimens weighed from 2.2 to 5.9 g, had no CLs or Type 1 or Type 2 corpora, and contained 8-22 total corpora, 12% of which were atretic. None were lactating. They are considered to have been postreproductive also.

Spotted dolphin specimens were judged to have been senescent when they had atrophic ovaries or

CONCLUSIONS

Several of our analyses have yielded results similar to those reported previously for spotted dolphins by others, notably Perrin et al. (1976) and Kasuya et al. (1974). We found ovulation rates to have high individual variability with a markedly higher rate of corpus formation in the earlier reproductive years that decreases after a fixed number of ovulations has occurred.

The conclusions reached by Perrin (1969b) and particularly by Kasuya et al. (1974) with regard to the close correlation between color pattern and sexual maturity in spotted dolphins are also supported by our study. Ninety-six percent of the fused, 50% of the mottled, and only 4% of the speckled specimens were sexually mature. Fused specimens had more corpora and appeared to have been sexually mature longer than mottled specimens of the same age or length.

Our estimated length of the calving interval (3.03 yr) is within the range of earlier estimates calculated for this stock by Perrin and Reilly (1984). It is also within the range of estimates for two other spotted dolphin stocks.

Some of our analyses, however, produced results

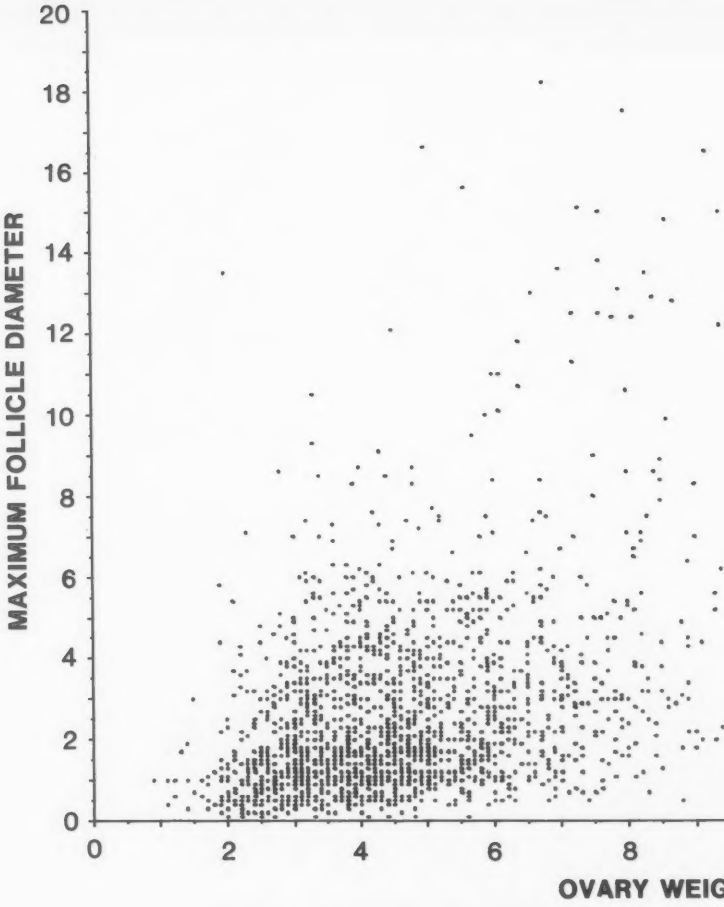

FIGURE 7.—Plot of maximum follicle diameter (mm) on combined ovary w

vary weight (g) for 3,464 female spotted dolphins.

that contradict earlier findings. Based on the more reliable method of estimating age in spotted dolphins, we believe that our findings present a clearer picture of the reproductive information than has been reported previously. Our aged samples showed that the youngest sexually mature female was 10 yr old—the same age as the youngest pregnant and the youngest lactating specimens. This suggests that some females must become sexually mature before the age of 10, even though mature specimens younger than 10 were not found in our sample. The average age of a pregnant female in our sample was about 18 yr, and some females of about 35 yr old were pregnant or nursing. These values are substantially higher than estimated previously for this stock (Perrin et al. 1976), but they are similar to, though still somewhat higher than, estimates for the western Pacific stock (Kasuya 1976).

The ASM estimate in this study (about 11.4 yr) is higher than that estimated by Perrin et al. (1976). Our calculations showed no significant difference between the ASM calculated for the 1973-74 sample (taken during years of heavy fishing mortality) and the ASM for the 1981 sample (taken after at least 5 yr of reduced fishing mortality).

An ASM of 11.4 yr means that the youngest average age of first parturition would be 12.3 yr (11 mo later). Since not all females would conceive at first ovulation, the actual average age would be greater than this. The implication of this protracted period before reproduction and a long (3.03 yr) calving interval is that spotted dolphin survival rates must be very high in order to maintain a stable population level.

There is a significant depression in the age structure of the 1973-78 and 1981 aged sample in the 6-12 yr age classes (Hohn and Myrick in prep.[2]). Similar age-structure patterns, interpreted as reflecting some sort of schooling segregation, have been encountered in studies of other delphinids (see review by Perrin and Reilly 1984). If animals at or near the age of sexual maturity have been regularly undersampled because their schools were not targets of purse seines (Hohn and Scott 1983), the ASMs calculated for the aged samples could be upwardly biased. However, there is no evidence that the depression in the age structure represents missing animals that were sexually mature.

The annual pregnancy rate averaged 0.33 from 1973 through 1981. There were no sustained upward or downward changes in age-specific pregnancy rates with increased age. A similar result was shown by Kasuya (1976) for the western stock, although his values were somewhat lower than the rates we have estimated for the northern offshore stock. Our estimates are different from those of Perrin et al. (1976) who reported high pregnancy rates among younger specimens and a decreasing rate with increased age.

The implications of an apparent progressive increase in the lactation period are enigmatic. It is probable that the increase in lactation period reflects the decrease in per capita mortality of calves due to the more efficient releasing procedures employed by the purse seine fleet from the mid-1970's onwards. Decreased mortality of nursing calves would be reflected by an apparent increase in the number of lactating females because fewer nursing periods were ended prematurely.

Our study of postreproductive specimens suggests that fertility diminishes as the complement of follicles for a female becomes expended through ovulation or atresia. Female spotted dolphins with atrophic ovaries or with no macroscopic follicles are reproductively senescent. Although the expenditure of follicles progresses with age, reduction in fertility is not strictly age related. The occurrence of reproductive senescence in spotted dolphins in this study was negligible and the number of specimens in this state probably is of limited importance to estimates of reproductive parameters.

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CHINOOK SALMON, *ONCORHYNCHUS TSHAWYTSCHA*, SPAWNING ESCAPEMENT BASED ON MULTIPLE MARK-RECAPTURE OF CARCASSES

STEPHEN D. SYKES AND LOUIS W. BOTSFORD[1]

ABSTRACT

Mark-recapture data from a population of chinook salmon, *Oncorhynchus tshawytscha*, carcasses were collected for escapement estimates in a northern California stream. Escapement was taken to be immigration into the population of carcasses. Results from three methods of estimating total immigration into this population—Jolly-Seber, Manly and Parr, and Jolly-Seber with a modified data set—were compared to a weir count. Sources of violations of modeling assumptions, age-dependent catchability, and survival were identified, but the estimates appeared to be relatively insensitive to these. The effect of lower sampling intensity, which exacerbates effects of age-dependent catchability, was evaluated through simulation. The third method appears to be the best of the three because 1) it requires the least sampling effort, 2) it is the most robust with respect to violations of the assumption of equal catchability, and 3) it enables reanalysis of previously collected data. Standard errors and 95% confidence intervals of estimates obtained by the third method were computed by simulation. Since the distribution of estimates is asymmetrical, these confidence limits are preferred over standard expressions.

Pacific salmon fisheries are currently managed by attempting to allow a specified number of fish to escape the fishery, migrate upstream and spawn. Proper management therefore requires accurate estimates of this escapement. Since Pacific salmon die immediately after spawning, escapement can be estimated from the number of carcasses that accumulate during a spawning season. The California Department of Fish and Game (CDF&G) estimates escapement of chinook salmon, *Oncorhynchus tshawytscha*, each year using the methods of Schaeffer (Schaeffer 1951; Darroch 1961) and Peterson (Seber 1982) to analyze mark-recapture data from surveys of accumulated carcasses. Since the fish enter the stream to spawn during the sampling periods, the assumption of a closed population required by the Peterson estimate does not hold. The Schaeffer method is designed to estimate numbers from a stratified two sample experiment in which fish are tagged at different locations (or different times at one location as fish migrate upstream) and are sampled at the same locations (or an upstream point) at a later time. CDF&G carcass surveys, on the other hand, involve sampling the same unstratified stretch of spawning stream several times. The results described here are part of an attempt to develop an accurate, efficient, and robust procedure for estimating escapement from carcass data. A technique that allows not just estimates for current and future years, but also could be used to analyze mark-recapture data taken by CDF&G in past years was desired.

Parker (1968) and Stauffer (1970) used standard Jolly-Seber methods to estimate spawning run sizes from mark-recapture data obtained from carcass counts. However, they did not examine departures from modeling assumptions by collecting appropriate data in the field or statistically testing assumptions. Also, an independent count of the population size was unavailable, hence actual errors in their estimates could not be computed. In addition, carcasses were carefully replaced where they had been found after sampling and tagging, hence captured carcasses would have a high probability of being recaptured. Thus, their results were probably biased because of heterogeneous capture probabilities.

To develop the estimation technique a mark-recapture experiment was performed in the Bogus Creek spawning area of the Upper Klamath River drainage during the 1981 chinook salmon spawning run. As a check on the estimates, a counting weir was placed at the mouth of Bogus Creek. Salmon were counted while they were in the weir trap, and were subsequently released upstream. This mark-recapture study differed from the usual mark-recapture studies of fish and wildlife populations in that the population was composed of carcasses (i.e., individuals enter the population by dying and leave by predation and decay). Thus, the age of a carcass,

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as used here, refers to time since death rather than time since recruitment.

The procedures followed here differed from previous CDF&G surveys in that more data were taken than were actually needed for the estimate so that departures from model assumptions could be examined. The additional data enabled simulation of the sampling procedure to estimate bias and variances, and allowed us to determine the sources of failure of assumptions. We were also able to develop estimates from which some sources of bias had been removed.

METHODS

The study was conducted on a chinook salmon spawning area of a small northern California stream, Bogus Creek (Fig. 1). The stream was sampled over a 6.5-mi reach from a counting weir upstream to Bogus School road. Sampling was begun on 15 September 1981, at the very beginning of the spawning run, and discontinued on 12 November 1981, by which time very little spawning activity was apparent. The stream was sampled weekly during that period; sampling took 2 d during the peak of the run, with one half of the stream being sampled per day. The stream was sampled by two people walking upstream and capturing with a gaff any carcasses seen. Data on each capture were described as follows:

Place of capture: Edge top, edge bottom, middle top, middle bottom, snagged, dry or buried.
Size: Small (<65 cm), medium minus (65-69 cm),

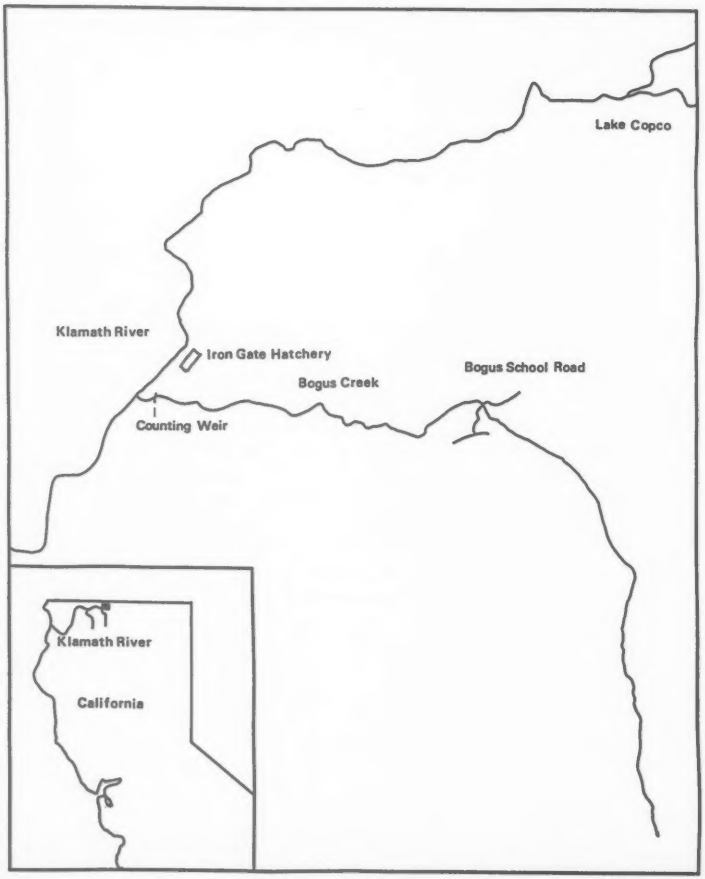

FIGURE 1.—Study area in northern California.

medium (70-80 cm), medium plus (81-85 cm), or large (>85 cm).
Sex: Male or female.
Condition: Alive, fresh (eyes clear), decayed minus (eyes cloudy, flesh firm), decayed (flesh soft), decayed plus (flesh very soft), or skeleton (flesh falling off).

Carcasses were individually tagged with fingerling fish tags which were attached around the maxillary bone. Data on place of release for each released carcass were recorded as follows:

Pool, pool/riffle, or riffle.
The presence or absence of obstructions which would trap and remove a carcass.
The speed of water flow.

Thus movements of individual carcasses and their condition, both of which might affect catchability and survival, could be examined on an individual basis. During the sampling process about one-third of the unmarked, captured carcasses was randomly removed from the population by cutting the fish in two. This was done because of limited time available for recording data. These individuals were considered "trap mortalities" (i.e., they are counted in the sample size but not in the total releases for that time period). Because the mark-recapture methods used allow for capture loss, removal of these fish has no effect on errors other than lowering sample sizes.

Two existing methods, those of Jolly and Seber (Seber 1982) and Manly and Parr (1968), and a third, a modified Jolly-Seber method, were used to estimate population sizes, recruitment, survival, and their standard errors (when expressions were available). The corrected estimates of Seber (1982) were used for the Jolly-Seber method. When survival was estimated as greater than unity, or immigration as <0.0, those values were replaced with 1.0 and 0.0 respectively in subsequent calculations. In the third method, standard Jolly-Seber estimates were calculated after modifying the mark-recapture data so that all decayed (decayed minus or worse) carcasses (marked and unmarked) were assumed to have been destroyed upon capture. This method simulates the way CDF&G has traditionally collected data.

After these estimates had been calculated, the estimated escapement, E, was calculated as the number present at the first sample period, plus the number of individuals immigrating during each subsequent period.

$$\hat{E} = n_1 + ((\hat{N}_2 - R_1 * \hat{\Phi}_1)/(\hat{\Phi}_1)^{.5}) + \hat{D}_2 + \hat{D}_3 + \hat{D}_4 \quad (1)$$

where n_1 = the number sampled at the first sample time,
R_1 = the number tagged and released at the first sample time,
$\hat{N}_2$ = the estimated population size at sample time two,
$\hat{D}_i = \hat{B}_i/(\hat{\Phi}_i)^{.5}$,
$\hat{\Phi}_i$ = the survival rate from i to $i + 1$, and
$\hat{B}_i$ = the estimated number of carcasses still present at the sample time $i + 1$ which immigrated between i and $i + 1$.

In this expression the initial number present at time period 1 is conservatively taken to be the sample size at time period 1 (n_1). The number immigrating during the subsequent period is taken to be the estimated population at time period 2, minus the number of tagged fish which had been accounted for in the first sample. Immigration during the next two periods are standard estimates. Each immigration rate is divided by the square root of the survival rate (the survival rate for half the sample period), to account for fish that enter the population and leave it between sampling periods, and thus are never sampled (Stauffer 1970).

Estimates of immigration during the last time period are not computed in standard multiple mark-recapture experiments; however, this immigration (B_4 here) can be estimated from the standard Jolly-Seber expression (Seber 1982), if the final numbers (N_5) and survival rate (Φ_4) can be estimated. If survival varies little from sample to sample, Φ_4 can be estimated by assuming that mortality is equal to the value estimated over an earlier period in this study. Since survival varied little between sampling periods and the χ^2 test of Seber (1982) failed to reject the null hypothesis of constant survival ($\chi^2 = 0.4648$, df = 2), we estimated survival from period 3 to period 4 as the average of $\hat{\Phi}_1$, $\hat{\Phi}_2$, and $\hat{\Phi}_3$. To estimate N_5, we estimated the capture probability at sample period 5 (P_5) as the ratio of the number of carcasses released at sample 4 and recaptured at sample 5 (r_4) to the number released at sample 4 (R_4) times survival to sample 5 ($\hat{\Phi}_4$),

$$\hat{P}_5 = r_4/(R_4 * \hat{\Phi}_4). \quad (2)$$

We then estimated the population size at sample 5

($\hat{N}_5$) as the sample size (n_5) divided by the capture probability ($\hat{P}_5$).

Standard errors and 95% confidence limits for the third method were obtained by simulation. The sampling process was simulated by generating a population of carcasses based on population size estimates from the third method. We then sampled the population by comparing a uniformly distributed random number with the appropriate probability of capture [see Sykes (1982) for a more detailed description of the simulation process, and a Fortran program].

From each simulation we calculated Jolly-Seber estimates of survival, immigration, population sizes, and their standard errors. An estimate of E was then calculated as above. This simulation process was repeated 1,000 times. In addition to calculating the average and standard error of each of these estimates, 95% confidence limits were calculated by Buckland's (1980) method 1. To obtain 95% confidence limits by this method, one adds the difference between the average of the 25th and 26th lowest estimates (out of 1,000) and the average value to the field estimate to obtain the upper bound and subtracts the difference between the average of the 25th and 26th highest estimates and the average value to obtain the lower bound.

All three methods assume that all individuals are equally catchable. The methods based on the Jolly-Seber model also assume that all individuals have equal probabilities of survival. Since violation of these assumptions could result in biased estimates, we determined whether catchability and survival varied and the effects of these on the estimates.

Several statistical tests can be used to check for differential catchability and mortality, but only among animals that are already marked. Two χ^2 tests, which compare expected frequencies of capture histories with actual frequencies (Seber 1982; Jolly 1982) were calculated from the unmodified field data. The test of Leslie and Carothers (Carothers 1971) was not performed because of the small number of sampling periods. Since both tests yielded expected values less than unity, pooled χ^2 values were also calculated, using a conservative df value of df = (number of pools − 1). For Seber's test, all values less than unity were pooled; for Jolly's, each value less than unity was pooled with the next highest value.

Following Leslie et al. (1953, cited by Seber 1982) we tested for homogeneity of catchability and survival by comparing estimates of population parameters obtained by different methods. These methods differ in sensitivity to survival and capture heterogeneity, hence the presence of heterogeneity should cause differences in estimates of the same parameter by the different methods. We tested the unmodified field data by calculating the following parameter estimates as per Leslie et al. (1953):

$\hat{v}_i$: the estimated number of new marks released at time i
$\hat{\Phi}_{\cdot i}$: the estimated survival for the subpopulation of marked carcasses, and
$\hat{N}_{\cdot i}$: the number of marked carcasses.

and compared them with, respectively,

v_i: the actual number of new marks released at time i
$\hat{\Phi}_i$: the Jolly-Seber estimate of survival, and
$\hat{M}_i$: the Jolly-Seber estimate of the number of marked carcasses.

If differential catchability or survival, when present, results in significant bias, these estimates will be different.

Since only marked (and thus decayed) carcasses are considered in the statistical tests discussed thus far, these tests do not address the potential for age-dependent catchability. To evaluate possible effects of age-dependent catchabilities we "corrected" the sample size n_i by reducing it to account for the fact that fewer fresh (shiny, silver colored) carcasses would have been captured if they had not been more visible than decayed (dull brown colored) carcasses. We then recalculated the escapement estimates using the corrected sample size. We used two ratios of average fresh to decayed catchability: 2.0 and 1.4. Since visibility only differed among carcasses on the stream bed, and only 30% of the captures were on the stream bed, these values represented actual ratios for carcasses on the stream bed of approximately 6.7 and 4.7, respectively.

To evaluate the potential advantage of increasing the efficiency of the third method by lowering the sampling effort we examined the effect of lowered sampling intensity on behavior of the three estimators. Lower effort would most likely result in less searching on the bottom of the stream for carcasses. We therefore simulated lowered sampling by generating new capture histories for each individual according to the following set of rules: 1) If an individual was buried at a capture event, that and all subsequent captures were ignored, 2) captures of decayed carcasses on the stream bed and surface were ignored according to comparison of a uniform random number with the appropriate decrease in capture probability, and 3) the next cap-

ture of an individual whose previous bottom capture was ignored was considered to be a bottom capture, as movement was probably the result of the previous capture event.

RESULTS

Total escapement estimates for the three methods and the weir count of fish moving into the spawning area are presented in Table 1. All three methods result in escapement estimates that are close to the weir count. The third method is the most efficient in the sense that it requires the least sampling effort.

TABLE 1.—Estimates of total escapement and the estimates used to compute them for each of the three methods.

	Jolly-Seber	Manly and Parr	Method 3
$\hat{N}_2$	999	1,076	1,063
SE $\hat{N}_2$	95	128	139
$\hat{N}_3$	2,302	2,312	1,886
SE $\hat{N}_3$	166	184	161
$\hat{N}_4$	1,845	1,853	1,452
SE $\hat{N}_4$	67	72	93
$\hat{B}_2$	1,801	1,740	1,459
SE $\hat{B}_2$	174	(1)	183
$\hat{B}_3$	150	136	371
SE $\hat{B}_3$	128	(1)	179
$\hat{\Phi}_2$	0.7617	0.7789	0.7297
SE $\hat{\Phi}_2$	0.353	(1)	0.439
$\hat{\Phi}_3$	0.7878	0.7940	0.8578
SE $\hat{\Phi}_3$	0.0305	(1)	0.0548
$\hat{n}_1$	87	87	87
$[\hat{N}_2 - R_1\hat{\Phi}_1]/\hat{\Phi}^{0.5}$	1,042	1,139	1,142
$\hat{D}_2$	2,062	1,970	1,708
$\hat{D}_3$	169	151	401
$\hat{D}_4$	84	91	170
$\hat{E}$	3,445	3,438	3,508
Weir count: 3,642			

[1]Estimate of these standard errors are not available.

For the third method, Jolly-Seber estimates and associated estimated standard errors, computed from the survey data along with the average value, standard errors, and 95% confidence limits obtained from simulation, are presented in Table 2. Estimated standard errors and simulated standard errors are in close agreement, except that the distribution of estimates around the mean value is clearly asymmetrical. Since they are based on simulation of the actual process rather than approximate analytical expressions, confidence limits obtained from simulation are presumably more realistic than those estimated by the methods of Jolly and Seber.

The sum of the estimated escapement by time $i + 2$ is plotted with the sum of the weir count at time i in Figure 2. Since the numbers of fish which migrated through the weir correlates well with the estimated number of fish that died 2 wk later, most salmon probably spawned and died within 2 wk of having entered the stream. Since the estimate of immigration during the last sampling interval seems to fit the known number of fish immigrating, the assumption of constant survival seems to be a good one. It is clear that our criteria for stopping sampling when most spawning activity had ceased resulted in an estimate of the complete run. Sampling for another week would have removed the need to make any assumptions in estimating B_4, but since this value will always be small in relation to the total escapement, the increase in accuracy does not seem worth the additional effort.

Data regarding the condition of carcasses at the time of capture reflect a declining trend in catch-

TABLE 2.—Estimates of escapement ($\hat{E}$), population size ($\hat{N}$), immigration ($\hat{B}$), survival ($\hat{\Phi}$), and associated standard errors obtained from a Jolly-Seber analysis of data for method three. Also shown are the computed mean, standard error, and 95% confidence intervals obtained by simulation.

		Simulation value			
	Field estimate	Mean	SE	Upper 95% C.I.	Lower 95% C.I.
$\hat{N}_2$	1,063	1,041	145	+222	−344
SE $\hat{N}_2$	139	138	43	+66	−100
$\hat{N}_3$	1,886	1,889	166	+289	−360
SE $\hat{N}_3$	161	165	28	+46	−62
$\hat{N}_4$	1,452	1,458	94	+167	−199
SE $\hat{N}_4$	93	94	19	+33	−43
$\hat{\Phi}_2$	0.7297	0.7327	0.0459	+0.0892	−0.0929
SE $\hat{\Phi}_2$	0.0439	0.0447	0.0021	+0.0039	−0.0046
$\hat{\Phi}_3$	0.8578	0.8559	0.0551	+0.1003	−0.1127
SE $\hat{\Phi}_3$	0.0548	0.0554	0.0090	+0.0145	−0.0205
$\hat{B}_2$	1,459	1,446	193	+360	−415
SE $\hat{B}_2$	183	189	29	+46	−68
$\hat{B}_3$	371	377	143	+307	−252
SE $\hat{B}_3$	179	143	22	+36	−53
$\hat{E}$	3,508	3,503	100	+186	+192

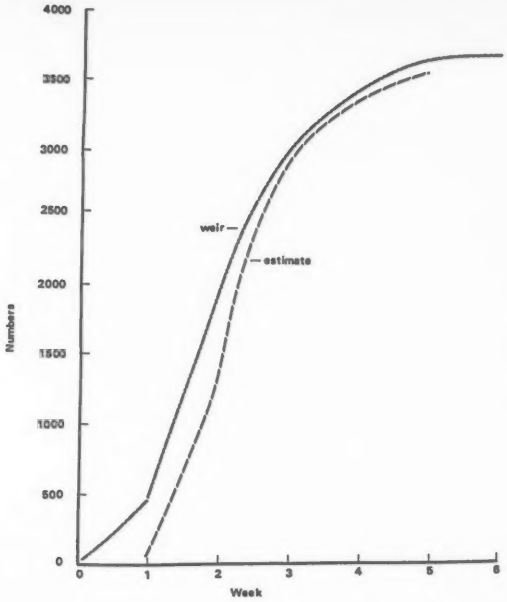

FIGURE 2.—Total numbers of fish immigrating as of week i by the weir count and total numbers of fish estimated by method three to have died as of week $i + 2$.

ability and/or survival with conditon among "marked" (and thus decayed) animals (Fig. 3). For each week, smaller and more decayed carcasses appear to have lower recapture rates. (Note that since this figure represents catchability at and after the earliest time of recapture, these data do not reflect catchabilities of fresh fish. Also, recapture rates for week 3 are higher than those for week 4 because there is one more opportunity for recapture.) These low recapture rates can be the result of either lower survival or lower catchability of smaller and more decayed carcasses. The effects of these differences in catchability on absolute numbers of recaptures would be small because of the small number of carcasses in the lower capture probability categories. Note also in Figure 3 that recapture rates of fresh carcasses vary less with size than decayed carcasses.

The expected and actual values for the tests for differential catchability and mortality, the contribution of each difference to the χ^2 value, and the normal and pooled χ^2 values are presented in Tables 3 (Seber 1982) and 4 (Jolly 1982), respectively. Although the fit between expected and observed values appears to be quite good, the total differences are statistically significant, hence catchability is not strictly homogeneous.

The comparison of estimated and actual parameters as suggested by Leslie et al. (1953, cited by Seber 1982) is presented in Table 5. The close agreement between both sets of estimates indicates any

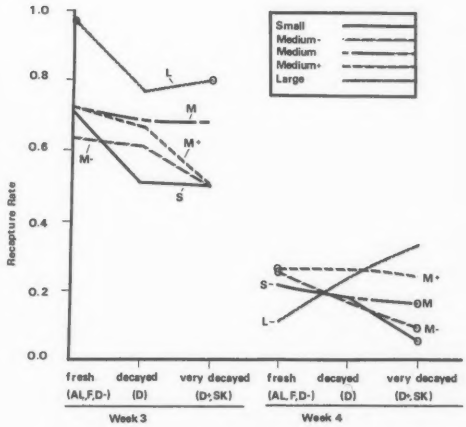

FIGURE 3.—Fraction of marked fish recaptured by size, condition, and week of release. Circled data points have sample sizes of numbers of fish recaptured <10. Where <5 fish were released, that point was not plotted. Note that all fish are decayed upon recapture. The "fresh" category here includes alive, fresh and decayed minus; the "decayed" category includes decayed and the "very decayed" category includes decayed plus and skeleton.

TABLE 3.—Expected [$E(b_w)$] and actual (b_w) numbers of individuals with the specific capture history w and the contribution of the difference between these values to the χ^2 test of Seber (1982). The listed capture histories indicate the fish was caught only at those times.

w	$E(b_w)$	b_w	$[E(b_w) - b_w]^2/E(b_w)$
2	120.22	116	0.1480
3	247.59	248	0.0007
4	589.01	588	0.0017
1,2	17.78	22	1.0000
1,3	2.37	2	0.0585
1,4	4.56	7	1.3121
1,5	0.30	2	9.4810
2,3	34.88	36	0.0362
2,4	66.97	68	0.0160
2,5	4.46	8	2.8045
3,4	359.38	355	0.0535
3,5	23.95	19	1.0225
4,5	150.07	153	0.0572
1,2,3	5.16	4	0.2603
1,2,4	9.91	9	0.0827
1,2,5	0.66	0	0.6601
1,3,4	3.44	2	0.6052
1,3,5	0.20	0	0.2295
1,4,5	1.16	0	1.1606
2,3,4	50.62	58	1.0749
2,3,5	3.37	5	0.7843
2,4,5	17.06	10	2.9266
3,4,5	91.56	102	1.1894
1,2,3,4	7.49	5	0.8267
1,2,3,5	0.50	0	0.4490
1,2,4,5	2.52	4	0.8636
1,3,4,5	0.88	0	0.8774
2,3,4,5	12.90	10	0.6511
1,2,3,4,5	1.91	2	0.0045
	$\chi^2 = 28.68$ df = 14	$\alpha = 0.025$	
Pooled	$\chi^2 = 17.06$ df = 10	$\alpha = 0.10$	

TABLE 4.—Expected and actual numbers of individuals caught at sample i and j ($m_{\cdot ij}$), regardless of their capture history before i and after j, and the contribution of the difference between these values to the χ^2 test for equal catchability and survival of Jolly (1982).

i,j	$E(m_{\cdot ij})$	$m_{\cdot ij}$	$[E(m_{\cdot ij}) - m_{\cdot ij}]^2/E(m_{\cdot ij})$
1,3	6.95	4	1.2510
2,3	117.05	120	0.0743
1,4	5.74	7	0.2752
2,4	96.74	91	0.3410
3,4	529.51	534	0.0380
1,5	0.31	2	9.2562
2,5	5.20	8	1.5064
3,5	28.49	24	0.7066
	$\chi^2 = 13.44$ df = 3	$\alpha = 0.005$	
Pooled	$\chi^2 = 6.34$ df = 2	$\alpha = 0.05$	

TABLE 5.—Estimates of the number of marks released (v_i), survival (Φ_i), and the marked population size ($\hat{n}_i$) for the standard Jolly-Seber method and the same estimates ($\hat{v}_i$, $\Phi_{\cdot i}$, $\hat{N}_{\cdot i}$, respectively) for the test for equal catchability and survival of Leslie et al. (1953, cited by Seber 1982).

Sample	v_i	$\hat{v}_i$	SE $\hat{v}_i$	Φ_i	$\Phi_{\cdot i}$	$\hat{M}_i$	$\hat{N}_{\cdot i}$
1	84	—	—	0.7995	—	67	—
2	311	—	—	0.7617	—	288	319
3	724	680	44	0.7878	0.7969	797	796
4	741	756	214	—	—	1,201	1,234
5	—	—	—	—	—	—	—

differential catchability or survival that does exist (as indicated by χ^2 tests and differential recapture rates) does not significantly bias resultant estimates.

Values of $\hat{E}$ computed from data "corrected" for age-dependent catchability are presented in Table 6. Again, it appears that if age-dependent catchability is present, it has little effect on the estimates. Also, that our estimates correlate well with the weir count estimates, whereas "corrected" estimates are far too low, indicates that this bias was probably not present in our sampling process. Thus biases encountered here are insignificant, both in relation to possible imprecision in estimating the percent run and area covererd, and the estimated standard errors.

Estimates computed to evaluate the effects of lowering sampling intensity are shown in Table 7. Simulations are listed according to the percent of top and the percent of bottom captures ignored for that simulation. The estimates obtained by the third

TABLE 6.—Escapement estimates obtained by correcting for differential catchability of fresh and decayed carcasses for three methods of estimating escapement. For each correction, the ratio of the average fresh to decayed catchabilities that was assumed to obtain the corrected estimate is given.

Assumed fresh/decayed Catchabilities	Corrected escapement		
	Jolly-Seber	Manly and Parr	Method 3
Original estimate	3,445	3,438	3,508
1.4/1.0	3,446	3,471	3,274
2.0/1.0	3,321	3,319	3,262

TABLE 7.—Escapement estimates obtained by simulation of reduced sampling effort for three methods of estimating escapement. For each simulation the fraction of decayed top carcass captures and the fraction of decayed bottom carcass captures ignored is given.

Fraction of decayed Carcass captures ignored		Escapement estimate		
Top	Bottom	Jolly-Seber	Manly and Parr	Method 3
Original estimate		3,445	3,438	3,508
0.0	0.4	3,740	3,765	3,676
0.0	1.0	3,944	4,058	3,777
0.2	0.4	3,890	3,917	3,977
0.4	0.6	4,844	4,934	4,364

method are less biased than those obtained by the other two methods.

DISCUSSION

The estimates of total immigration are all remarkably close to the weir count. This accuracy is even more remarkable in light of the fact that CDF&G has traditionally used a correction factor of 0.95 to account for an estimated 5% of the spawning grounds that is not sampled on Bogus Creek. Inclusion of this factor brings all of the estimates to within 1.4% of the weir count. Since the third method provides a high degree of precision (Table 2) at much less sampling cost, it is preferable over the other two methods. We can compare the precision of the third method with the Jolly-Seber and Manly and Parr methods by comparing the standard error estimates that are available for those two methods (Table 1). The Jolly-Seber method is more precise in estimates of N, B, and Φ. This is expected, since both the Manly and Parr method and the third method use fewer individuals in estimates than the Jolly-Seber method does. However, the precision of the third method is more than adequate: 95% confidence intervals are +5.3% and −5.5% of the escapement estimate.

The detected violations of assumptions, age-dependent catchability and heterogeneity of capture probabilities and survival, are those that would be expected on the basis of physical considerations. Survival of carcasses is a function of two processes: fresh carcasses being removed by carnivores, and old carcasses decaying and becoming buried in the stream bed. Rates of disappearance could thus be affected by condition, and therefore age and size, of carcasses. Older carcasses and smaller carcasses, which decay more quickly and are buried more easily than larger carcasses, would be expected to have lower survival rates.

Catchability is a function of both visibility and location, both of which would be expected to vary with condition and size of carcasses. This causes two different types of problems: age-dependent catchability and size-dependent catchability. Shiny, fresh carcasses were much more visible on the bottom of the stream than the brown, decayed carcasses. Carcasses on the stream surface were in general visible regardless of their condition. Since carcasses lost their high visibility in about a week, no marked carcasses will be in this high visibility category, and unmarked carcasses will on the average be more catchable than marked carcasses. This can be thought of as age-dependent catchability. Size-dependent catchability stems from the fact that decayed individuals that were large were more visible than those that were small. This can be viewed as capture heterogeneity. Since fresh fish were high visible regardless of their size, this heterogeneity existed only among decayed individuals. Based on these considerations we would expect catchability to vary with age and size according to Figure 4.

While both Jolly's (1982) and Seber's (1982) tests indicate differential catchability and/or mortality are present, the issue of real importance is the amount of any resulting bias. Manly (1970) concluded that if age-specific mortality is present in a sampled population, Manly and Parr (1968) estimates should fare better than those of Jolly and Seber (Seber 1982). Both methods, however, are biased for the case in which mortality increases with age; in fact, Manly's (1970) estimates of bias for additions (B) are greater for Manly and Parr estimates than for Jolly-Seber estimates for those simulations with parameters closest to our population. Survival, population size, and catchability estimates were negatively biased by only 1 or 2%. Seber (1982) pointed out that Jolly-Seber estimates should be relatively unbiased even with differential mortality if mark status and mortality were not correlated. Both estimators, then, should have relatively unbiased estimates of survival and catchability for "marked" animals. A positive bias in estimates of immigration, B, (and consequently in $\hat{E}$) would arise primarily from applying mortality of marked animals to the entire population, when marked animals are in general older, and thus have lower survival than unmarked animals.

The age-dependent catchability detected in this study would be expected to result in a positive bias in the estimate of total escapement, E. Because each capture sample includes fresh, recently immigrated individuals, and recapture samples include older, decayed individuals, we expect N to be overestimated (i.e., $n/N > m/M$ in Jolly-Seber and $pN < n$ in Manly and Parr), which results in estimates of B and E being positively biased also. Since bias from age-dependent catchability in N decreases as M approaches N, and removing carcasses after capture in the third method decreases the ratio of marked to total carcasses, we would expect the third estimator to be more biased by age-dependent catchability problems than the first two methods.

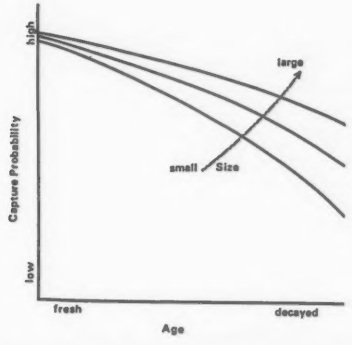

FIGURE 4.—Expected changes in capture probabilities with age at different sizes.

However, the simulations of lower sampling intensity, which would exacerbate the effects of age-dependent catchability, show that the estimate obtained by the third method is more robust with regard to lowered sampling intensity. This unexpected result is probably due to compensating effects which decrease bias in E. The two most important components of E are the second ($(N_2 - R_1 \hat{\Phi}_1)/\hat{\Phi}_1^{.5}$) and third ($\hat{D}_2$). In the standard estimates these values both increase with increases in the number of captures ignored. In the third method, however, the second component increases, but the third decreases. This is because as catchability declines, fewer marks are captured and "removed", hence more carcasses are available for later capture. This is not the case in the first two methods because marked carcasses are not removed at capture. Since in the third method the composition of M and N is relatively unchanged at the second sample period, but at the third sample period, M increases relative to N (because of the increase in the number of decayed marks present), the estimate of population size at the third sample period will be less biased than the estimate for the second sample period. This results in a negative bias in the estimated immigration from time period two to three. This compensation makes the third method more robust with respect to age-dependent catchability problems than the other two methods. Bias in the estimates is not severe until large numbers of capture events are ignored (Table 7). While all three methods produce accurate estimates, even when lowered sampling exacerbates differential catchability problems, the magnitude of the bias relative to standard errors can be substantial. For this reason, samples must be carefully taken if estimates from different streams or different years (which will have different biases because of different conditions) are to be compared statistically.

Heterogeneity of capture probabilities affects Jolly-Seber and Manly and Parr estimates in the same manner. Since in the Jolly-Seber method the individuals marked and released at sample i, R_i, are on the average younger than the individuals marked and released prior to sample i, M_i is a low estimate (i.e., $r/R > z/(M - m)$, or $M > (Rz/r) + m$). This decreases the positive bias in N which is caused by age-dependent catchability. Since bias in M increases as more individuals are marked, we expect

estimates of M from the third method to be less biased than those from the first two.

Usually, capture heterogeneity leads to the more catchable animals joining the marked population, and we expect marked animals to be more catchable than unmarked animals. Capture heterogeneity, however, is only prevalent among decayed individuals who are all less catchable than fresh, unmarked individuals. Thus, capture heterogeneity, by placing the more catchable decayed individuals in the marked population, results in the capture probability of marked animals being closer to the capture probability of unmarked animals. This reduces the negative bias in population size (N), immigration (B), and escapement (E) estimates, which was caused by age-dependent catchability. Again, the third method, by removing decayed individuals and decreasing the fraction of the population which is decayed, will not be affected by capture heterogeneity as strongly as the other two methods.

Manly and Parr estimators will have the same ameliorating affects because of capture heterogeneity as their Jolly-Seber counterparts. Since the estimate of catchability, p, should be accurate for the more catchable animals, estimated survival should be accurate for that group. Bias would result from correlations between catchability and survival. Also, since p is estimated for marked (and thus decayed) individuals, using the more catchable decayed individuals to estimate p brings the estimated catchability closer to the actual catchability of the unmarked individuals. Again, this reduces the bias in $\hat{N}$, $\hat{B}$, and $\hat{E}$ which is caused by age-dependent catchability.

There are other approaches to estimating parameters from populations with age-dependent survival and capture rates. By placing carcasses in two readily identifiable age classes, fresh (and thus <1 wk old) or decayed (and thus older than 1 wk), Pollock's (1981) modified Jolly-Seber analysis of the data could have been made. Since this method requires recaptures of decayed individuals, it could not be used to analyze data from previous surveys, and it would require more sampling effort in future surveys than the method 3 estimate. If different age classes have sufficiently different capture or survival rates, then this method will provide more accurate estimates. If not, then it will yield the same estimate as the third method, but would have higher variances, as more parameters are estimated.

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THE DISTRIBUTION OF THE HUMPBACK WHALE, *MEGAPTERA NOVAEANGLIAE*, ON GEORGES BANK AND IN THE GULF OF MAINE IN RELATION TO DENSITIES OF THE SAND EEL, *AMMODYTES AMERICANUS*

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ABSTRACT

The distribution of the humpback whale, *Megaptera novaeangliae*, (based on shipboard sighting data) is significantly correlated ($r = 0.81$, df = 13) with the number of sand eel, *Ammodytes americanus*, per standardized tow (based on NMFS/NEFC groundfish surveys) by strata within the Gulf of Maine. A demonstrated increase in the number of humpback whale sightings in the southwest Gulf of Maine since 1978 concurrent with an increase in the number of sand eel in the same area supports the hypothesis that within the Gulf of Maine the present distribution of humpback whales is due to the distribution of their apparent principal prey, the sand eel. A similar correlation between humpback whale sightings and sand eel abundance on Georges Bank was not significant ($r = 0.24$, df = 18) despite dense patches of sand eel in that region. Therefore, within the combined Gulf of Maine-Georges Bank regions, factors other than simply prey availability must influence the feeding distribution of the humpback whale. We argue that the bottom topography of the Gulf of Maine and the foraging behavior of the whales are critical factors influencing their present feeding distribution.

In the northwest Atlantic, the major summer concentrations of humpback whales, *Megaptera novaeangliae*, occur off the coasts of Newfoundland-Labrador and off the coast of New England in the Gulf of Maine which includes Georges Bank (Katona et al. 1980; Whitehead et al. 1982). During this period feeding is their principal activity. The major winter concentrations in the western North Atlantic occur along the Antillean Chain in the West Indies, principally on Silver and Navidad Banks which lie north of the Dominican Republic (Winn et al. 1975; Balcomb and Nichols 1978; Whitehead and Moore 1982). During this season conception and calving are their primary activities; food does not seem to be an important determinant of the humpbacks in these areas (Whitehead and Moore 1982).

Humpbacks have been generally considered coastal animals (Mackintosh 1965). However, their migratory routes between regions of winter breeding and summer feeding in the northwest Atlantic (based on sighting data) occur in deeper, slope waters off the continental shelf (Hain et al. 1981; Kenney et al. 1981; Payne et al. 1984). Several possible offshore routes between winter and summer grounds suggest reasonably distinct stocks (Katona et al. 1980). Kenney et al. (1981) suggested that for the Gulf of Maine stock, the Great South Channel (Fig. 1) is the major exit-entry between the Gulf of Maine feeding area and the deeper, offshore migration route.

Humpback whales have been described as generalists in their feeding habits (Mitchell 1974). The reported prey of humpbacks in the Gulf of Maine are Atlantic herring, *Clupea harengus*; Atlantic mackerel, *Scomber scombrus*; pollock, *Pollachius virens*; and the American sand eel, *Ammodytes americanus* (Gaskin 1976; Katona et al. 1977; Watkins and Schevill 1979; Kraus and Prescott 1981). In recent years, observations of feeding humpbacks indicate that sand eels have become an increasingly important prey item in the Gulf of Maine (Overholtz and Nicolas 1979; Hain et al. 1982; Mayo 1982).

Kenney et al. (1981) hypothesized that the observed distribution of the Gulf of Maine humpback stock was due to the distribution of sand eel, their apparent principal prey species. However, the present distribution of the humpback whale in the Gulf of Maine and throughout the remaining shelf waters of the northeastern United States is not so clearly related to the distribution of sand eel as was suggested. Although we recognize an important predator-prey interaction between humpbacks and sand eel, we hypothesize that behavior and bottom

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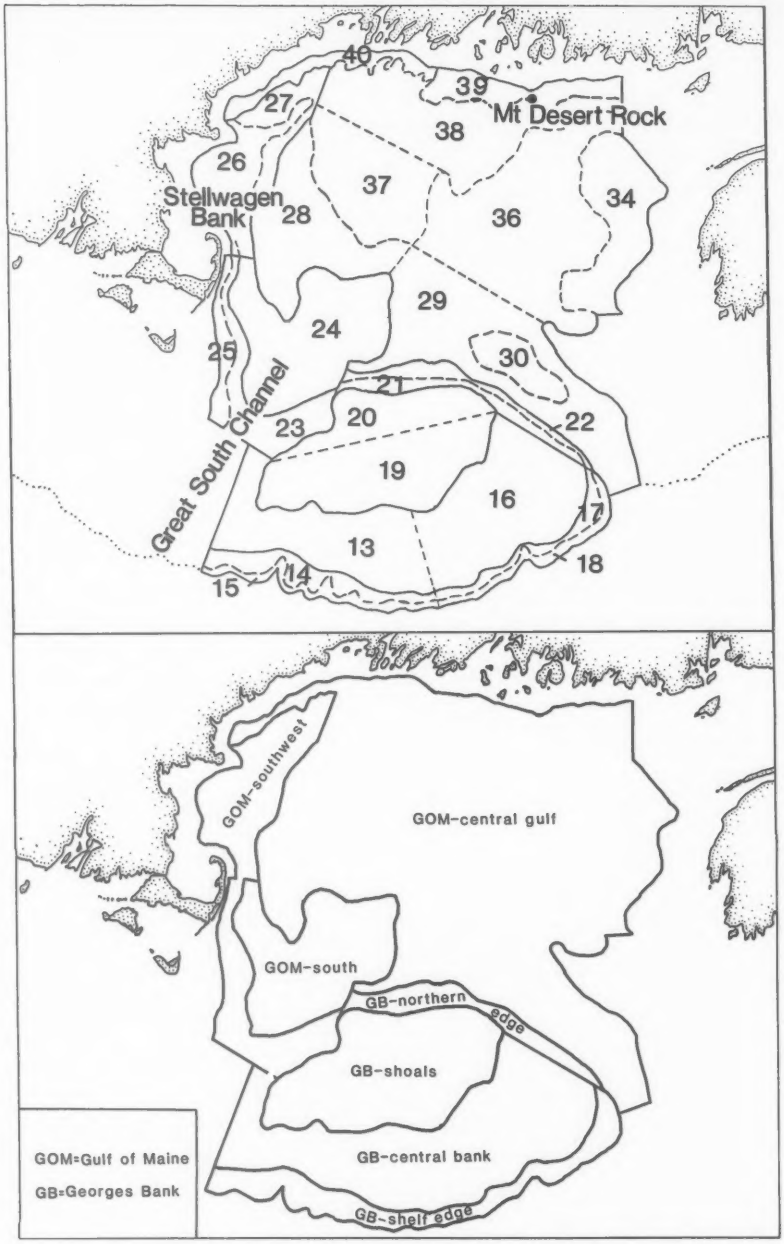

FIGURE 1.—The geographical areas and NMFS/NEFC bottom-trawl survey strata in the study area (upper) and the combined strata into regions (lower) referred to throughout the text.

topography are also critical factors in the foraging strategy of humpbacks, hence the present distribution of these whales. We base this hypothesis on observed sightings of humpbacks throughout the shelf waters of the northeastern United States in relation to sand eel abundance, and on an apparent shift in the center of feeding areas used by humpbacks in the Gulf of Maine since the mid-1970's.

METHODS

The collection of fisheries data used in these analyses was carried out by National Marine Fisheries Service/Northeast Fisheries Center (NMFS/NEFC) scientists and technicians on domestic research vessels during standardized spring bottom-trawl surveys. These surveys measure trends in finfish population abundance and have been used to monitor changes in the size and composition of finfish biomass (Clark and Brown 1977; Grosslein et al. 1980).

Meyer et al. (1979) found that spring (March-May) bottom-trawl surveys accurately reflect trends in sand eel abundance. Therefore, the fisheries data we examined were from these surveys, 1978-82. The stratified mean catch per tow of sand eel was calculated for each region and considered proportional to the population size within each region. We transformed the mean catch into logarithmic values; then, using a two-way analysis of variance (F-statistic), we compared sand eel population size by region and year.

The survey area includes shelf waters from Cape Hatteras north to Nova Scotia and has been spatially stratified by the NMFS/NEFC, based principally on depth and latitude (Grosslein 1969). Sampling stations are randomly assigned within a stratum and the number of stations allocated to strata approximately in proportion to the area of each stratum (Grosslein 1969). In this study, individual stratum have been combined into regions (Fig. 1), in a manner consistent with NMFS/NEFC management units. The two important regions emphasized are the Gulf of Maine and Georges Bank.

Sightings of humpback whales were recorded by observers from the Manomet Bird Observatory (MBO) on NMFS/NEFC research vessels conducting standardized surveys. Observations were recorded continuously along the predetermined cruise path between the sampling stations (following Payne et al. (1984)) in 15-min periods where each period represents a transect. Thus, the duration of each observation period was constant, but the linear km surveyed within each 15-min period depended upon vessel speed. The location (latitude-longitude) of each 15-min observation and the location and number of humpback whales observed were recorded and assigned to appropriate regions to facilitate direct comparisons between the observed number of humpbacks per linear km (humpbacks/effort) and potential prey densities.

Humpback whales are generally present in the study area from spring through fall (March-November) and absent during the winter (CETAP 1982). Therefore, sighting data and effort for winter months were excluded from the analyses. We also examined sighting data collected only during optimum sea conditions less than Beaufort (Kenney et al. 1981) (<16 nmi/h). Difference between the number of humpbacks/effort sighted by region and year were also compared by a two-way analysis of variance (F-statistic).

A coefficient of correlation (r) from the linear regression between the stratified mean catch of sand eel (log) and the number of humpbacks/effort was used to determine whether concentrations of humpback whales co-occurred with patches of sand eel within regions of the Gulf of Maine and Georges Bank.

A $P < 0.05$ was considered statistically significant.

RESULTS

Distribution of Sand Eel

The stratified mean number of sand eel varied significantly between regions on Georges Bank ($F = 14.14$, $df = 3, 12$) and in the Gulf of Maine ($F = 16.90$, $df = 2, 8$). On Georges Bank, sand eel were very abundant on the shoals with catches ranging from 1.117 sand eel/tow (log value) in 1978 to 2.846 (log value) in 1982 (Table 1). Sand eel were absent from most tows along the northern and shelf edges. Sand eel were also abundant in the southwest Gulf of Maine ranging from 0.670 sand eel/tow (log value) in 1978 to 2.422 in 1981 (Table 1). Sand eel were not abundant in the deeper, central Gulf of Maine. This patchy distribution reflects a known preference of the sand eel for sand-bottom substrates (Bigelow and Schroeder 1953) characteristic of submarine banks and shoals. No significant differences were found between the stratified mean catch per tow (log value) by year.

Distribution of Humpback Whales

Since 1978, the observed number of humpbacks/effort in the Gulf of Maine has steadily increased

TABLE 1.—Stratified mean number of sand eel per tow ± SE (in parentheses) and the number of sampling tows (lower number) by region and year.

Region	1978	1979	1980	1981	1982
Georges Bank					
shoals	1.117	1.200	2.752	1.850	2.846
	(0.233)	(0.305)	(0.590)	(0.499)	(0.691)
	15	30	15	15	15
northern edge	0.000	0.256	0.000	0.747	0.000
	—	(0.211)	—	(0.464)	—
	9	16	8	8	8
shelf edge	0.100	0.000	0.000	0.000	0.000
	(0.707)	—	—	—	—
	15	14	14	10	14
central bank	0.941	0.410	0.236	0.654	0.034
	(0.182)	(0.202)	(0.132)	(0.396)	(0.341)
	21	38	18	19	19
Gulf of Maine					
central gulf	0.000	0.012	0.141	0.055	0.000
	—	(0.012)	(0.101)	(0.545)	—
	64	61	47	45	47
southern	0.000	0.625	0.116	1.077	0.116
	—	(0.422)	(0.115)	(0.617)	(0.115)
	9	12	6	6	6
southwest	0.670	1.286	1.240	2.422	0.860
	(0.371)	(0.289)	(0.384)	(0.756)	(0.318)
	20	34	16	18	21

(Table 2). Over 90% of the humpbacks/effort observed each year in the combined Georges Bank-Gulf of Maine waters were seen in the Gulf of Maine. The increased number of humpbacks/effort observed was significantly different between regions in the Gulf of Maine ($F = 7.098$, $df = 2, 8$). The greatest concentrations of humpbacks in the Gulf of Maine are located in the southwest region (Table 2). Between 1978 and 1982, 82% of the total humpbacks/effort in the Gulf of Maine were observed in the southwest region. The importance of this region for feeding humpbacks has been previously reported (Kenney et al. 1981; Hain et al. 1982).

Although there were no significant differences between the number of humpbacks/effort seen by year ($F = 0.824$, $df = 4, 12$) or region ($F = 0.609$, $df = 3, 12$) on Georges Bank, the number of humpbacks/effort observed on the bank has steadily declined since 1978. Sixty percent of the humpbacks/effort observed on Georges Bank between 1978 and 1982 occurred during 1978 (Table 2).

We examined the apparent increase in the southwest Gulf of Maine more thoroughly by dividing it into two smaller components (Table 3), a southern which extends from the Great South Channel north along the outside of Cape Cod (NMFS/NEFC strata 23, 25, from Figure 1) and a northern which centers on Stellwagen Bank (NMFS/NEFC strata 26, 27, from Figure 1). The number of humpbacks/effort observed within the southwest Gulf of Maine-northern segment steadily increased by an order of magnitude from 1.86×10^{-2} whales/effort in 1978 to 29.01×10^{-2} whales/effort in 1982. Therefore, the observed increase in the number of humpbacks/effort in the southwest Gulf of Maine since 1978 has occurred primarily in the northern half of this region (NMFS/NEFC strata 26, 27).

TABLE 2.—The number of humpback whales per linear km $\times 10^{-2}$ (humpbacks/effort) seen during shipboard observations and the total number of linear km surveyed (in parentheses) by region and year.

Region	1978	1979	1980	1981	1982
Georges Bank					
shoals	—	0.189	—	—	—
	(480.9)	(529.0)	(190.0)	(342.6)	(744.5)
northern edge	1.500	—	—	—	—
	(200.0)	(176.8)	(66.5)	(89.8)	(222.7)
shelf edge	—	—	—	—	0.225
	(230.0)	(213.6)	(115.6)	(207.0)	(198.6)
central bank	0.168	0.285	0.299	—	0.116
	(593.6)	(701.9)	(334.4)	(895.9)	(863.5)
Gulf of Maine					
central gulf	0.750	0.119	—	0.855	—
	(933.1)	(841.7)	(966.0)	(467.6)	(1,172.8)
southern	2.449	0.828	—	0.393	1.662
	(489.8)	(482.8)	(267.6)	(254.2)	(223.5)
southwest	1.174	2.817	7.679	11.172	6.814
	(681.2)	(745.4)	(547.0)	(454.9)	(692.5)

TABLE 3.—The number of humpback whales per linear km $\times 10^{-2}$ (humpbacks/effort) seen during shipboard observations and the total number of linear km surveyed (in parentheses) within the partitioned southwest Gulf of Maine.

Region	1978	1979	1980	1981	1982
Northern	1.864	2.655	10.794	22.469	29.014
(strata 26, 27)	(34.9)	(263.6)	(333.5)	(252.6)	(299.6)
Southern	0.556	3.113	2.811	1.987	3.308
(strata 23, 25)	(359.3)	(481.8)	(213.5)	(202.3)	(392.9)

Correlation Between Humpback Whale Distribution and Sand Eel Abundance

A significant correlation ($r = 0.81$, $df = 13$) exists between the observed number of humpbacks/effort and the log-mean number of sand eel/tow by region within the Gulf of Maine (Fig. 2). This indicates that within the Gulf of Maine the distribution of humpback whales do co-occur with dense patches of sand eel in that region. The greatest densities of sand eel in the Gulf of Maine and the greatest observed numbers of humpbacks/effort have both occurred in the southwest Gulf of Maine since 1978. This supports the hypothesis by Kenney et al. (1981) that within the Gulf of Maine, the

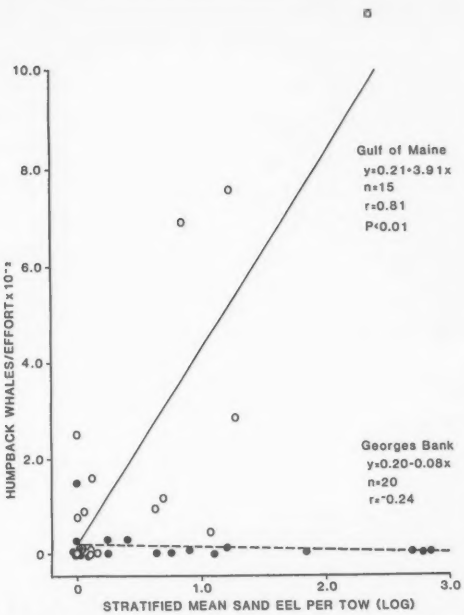

FIGURE 2.—The regression and correlation coefficient (r) between the stratified mean number of sand eel/tow (log value) and the number of humpback whales/effort $\times 10^{-2}$ by region and year on Georges Bank (closed circles) and in the Gulf of Maine (open circles).

observed distribution of the humpback whale was due to the distribution of sand eel.

However, the correlation between the observed number of humpbacks/effort and the log mean number of sand eel/tow by region on Georges Bank (Fig. 2) was not significant ($r = 0.24$, df = 18). The mean number of sand eel/tow (log value) on Georges Bank was greatest on the shallow shoals. Only one humpback whale was observed on the shoals between 1978 and 1982. Our data does not support any co-occurrance between humpback whale distribution and sand eel abundance on Georges Bank despite dense patches of sand eel in that region.

DISCUSSION

Our data suggest that the distribution of humpback whales in the Gulf of Maine-Georges Bank region is presently centered in the southwest Gulf of Maine. This distribution is correlated with dense concentrations of sand eel, a principal prey item, which has dramatically increased throughout shelf waters of the eastern United States including the southwest Gulf of Maine since the mid-1970's (Meyer et al. 1979; Sherman et al. 1981). This increase in sand eel followed a decline of Atlantic herring stocks from the mid-1960's to the mid-1970's (Anthony and Waring 1980; Grosslein et al. 1980), and possible replacement by sand eel of depleted fish stocks in the northwest Atlantic (Sherman et al. 1981). The correlations between the humpback distribution in the Gulf of Maine and sand eel abundance supports the theory by Kenney et al. (1981) that the present distribution of the whales in that region is due to the distribution of sand eel. A demonstrated shift in the humpback distribution since the mid-1970's from the upper Gulf of Maine-lower Bay of Fundy southward into the southwest Gulf of Maine also supports this theory.

A 10-yr summary of observations from Mt. Desert Rock, ME (MDR, Fig. 1) in the northern Gulf of Maine shows a dramatic decrease in the number of humpback sightings/observer hour since 1977 (Mullane and Rivers 1982). The maximum number of humpbacks observed in that summary occurred in 1975 (98 whale sightings, 0.123 humpbacks/observer hour). Only 10 humpbacks were seen from 1978 to 1982, and the maximum number of humpbacks/effort since 1975 has been 0.005/observer hour in 1982. This decline in the number of humpbacks at MDR coincides with the increased numbers of humpbacks observed in the southwest Gulf of Maine. Twelve of the 17 humpbacks photo-identified from 1975 to 1977 at MDR have subsequently been seen in the southwest Gulf of Maine, principally on Stellwagen Bank. At least three of these whales have been observed during three different years on Stellwagen Bank since they were first identified at MDR (Mullane and Rivers 1982). In comparison, only one whale identified at MDR has consistently returned to the coastal waters of eastern Maine and New Brunswick. Katona et al. (1977) also listed the Grand Manan Banks, Briers Island-St. Mary's Bay, Nova Scotia, and the lower Bay of Fundy as areas of humpback congregations. However, humpbacks were not common in the Bay of Fundy during 1981 and 1982 (Kraus and Prescott 1981, 1982).

Shifts in the distribution of humpbacks caused by changes in the distribution and density of prey species have been shown elsewhere (Lien and Merdsoy 1979; Whitehead et al. 1980). We believe that the correlations between humpbacks/effort and mean sand eel catches in the southwest Gulf of Maine, and the demonstrated decline of humpbacks throughout the upper Gulf of Maine-lower Bay of Fundy concurrent with an increase in the numbers

of humpbacks in the southwest Gulf of Maine reasonably explains the present distribution of humpbacks within the Gulf of Maine. However, it does not adequately explain the paucity of humpbacks on Georges Bank (Table 2) and throughout the remaining shelf waters of the northeastern United States (Hain et al. 1981; Kenney et al. 1981; Payne et al. 1984), areas where sand eel have also increased since 1975. The nonsignificant correlation between humpbacks/effort and the log-mean catches of sand eel/tow on Georges Bank suggests that factors other than simply food concentrations, perhaps behavioral or environmental, may influence the humpback's feeding strategy and location.

Sutcliffe and Brodie (1977) reported that humpbacks are led into ecological or oceanographic boundaries (i.e., isopleths or shelf-edges) and feed in patchy areas of dense prey aggregations along these boundaries. A change in depth on the shelf is often accompanied by a concentration of near-surface zooplankton; in general, the more abrupt the change, the greater the concentration (Sutcliffe and Brodie 1977). Concentrations are especially noticeable along the edge of banks where the availability of prey is most affected (Jaansgard 1974). Reay (1970) found that sand eel concentrations are greatest on the edges of sandy banks where currents and prey (zooplankton) are optimum; thus the whales, in seeking the highest concentrations of prey, feed most frequently along the edges of the banks (Sutcliffe and Brodie 1977; Brodie et al. 1978). Observations of feeding humpbacks in the Gulf of Maine have occurred primarily along the edge of submarine banks or canyons (Hain et al. 1982; CETAP 1982).

If bottom topography influences feeding behavior of humpbacks (by concentrating prey), then the paucity of humpbacks on Georges Banks and throughout the mid-Atlantic Bight regions becomes more understandable. The floor of the broad mid-Atlantic Bight is gently sloping continental shelf with no relief until it steepens sharply at the shelf break, at about 200 m depth, to form the continental slope. Since the feeding behaviors for humpbacks described by Hain et al. (1982) occur principally over a shelf-floor with rugged relief, the strategies used by humpbacks seem most efficient in these waters. This also explains the present lack of sightings in the mid-Atlantic shelf waters and the offshore migration route between calving and feeding areas. It seems energetically advantageous for the humpback, a relatively slow-moving whale, to migrate over deep water with little apparent feeding, then feed on the densely concentrated prey along the bottom profiles of the Gulf of Maine.

We maintain that humpbacks are merely utilizing the first concentrations of prey available to them in spring, after they reach shelf-waters from their offshore migration route between winter-calving and summer-feeding grounds. The humpbacks seem to use the Great South Channel as an entry-exit into the Gulf of Maine (as hypothesized by Kenney et al. (1981)), and follow the bottom profile northward, using this profile to their feeding advantage until they reach the dense concentrations of sand eel available within the southwest Gulf of Maine. The quantities of sand eel available to humpbacks at this location have allowed the whales to remain throughout the feeding season; therefore, the recent paucity of sightings in the northern Gulf of Maine.

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SEABIRDS NEAR AN OREGON ESTUARINE SALMON HATCHERY IN 1982 AND DURING THE 1983 EL NINO

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ABSTRACT

In the summer of 1982, 14.4 million salmon, *Oncorhynchus* sp., smolts were released at the Yaquina Estuary, OR; and in the summer of 1983, 12.8 million salmon smolts were released. Within hours after release, fish-eating seabirds aggregated at the estuary mouth. In 1982, the number of no seabirds was significantly correlated with the number of days since a release. In 1983, however, numbers of common murres, *Uria aalge*; gulls, *Larus* sp.; and brown pelicans, *Pelecanus occidentalis*, were significantly inversely correlated with the date of a release, and the number of cormorants, *Phalacrocorax* sp., was significantly more abundant the second day after a release. In contrast, numbers of Caspian terns, *Sterna caspia*, and pigeon guillemots, *Cepphus columba*, showed no relationship with releases in 1983.

There were significantly more cormorants and marbled murrelets, *Brachyramphus marmoratus*, in 1983 than in 1982. There were also significantly more murres in 1983 than in 1982 before 1 August, but fewer afterwards. Gull and brown pelican numbers were about the same between years, but significantly fewer pigeon guillemots were present in 1983 than in 1982.

Seabirds have been estimated to consume 29% of the pelagic fish production within 45 km of a British seabird colony (Furness 1984b), and several simulation models for various geographical areas indicate that 20-30% of the annual pelagic fish production may be preyed upon by seabirds (Furness 1984a). Since the mortality of salmon, *Oncorhynchus* sp., smolts as a result of predation and environmental factors is greater shortly after they first enter the ocean than after they move offshore (Parker 1962, 1968), the impact of seabird predation on salmon smolts just released along a coast could also be significant.

El Nino is the intrusion of anomalously warm water off the coast of Peru and Ecuador (Barber and Chavez 1983); an El Nino of varying intensity occurs on the average of every 3-5 yr (Quinn et al. 1978; Duffy 1983a). Along the Oregon coast, warm-water conditions concurrent with an El Nino appear much more rarely, and in the last century have occurred only in 1983, 1957-1958, and perhaps in 1941 (Huyer 1983; Reed 1983). The impact of seabirds on hatchery-released salmon smolts would be expected to be greater in years of anomalously warm water associated with El Nino, when natural prey for seabirds become rare and seabirds starve or have low nesting success (Boersma 1978; Duffy 1983a, b; Ainley 1983; Schreiber and Schreiber 1984).

Here, I correlate bird numbers with salmon smolt releases at Yaquina Estuary, OR, and examine variation in bird numbers between the summer of 1982 and the summer of 1983, when warm water associated with an El Nino was present.

STUDY AREA AND METHODS

Yaquina Estuary (Fig. 1) is located on the mid-Oregon coast and is a drowned river valley. It has an intertidal and submerged area of 15.8 km^2 (Oregon State Land Board 1973). During this study, all releases were from the site designated as OAF in Figure 1.

The most abundant seabird nesting nearby was the common murre, *Uria aalge*, but western gulls, *Larus occidentalis*; Brandt's cormorants, *Phalacrocorax penicillatus*; pelagic cormorants, *P. pelagicus*; and pigeon guillemots, *Cepphus columba*, also nested there (Table 1; Pitman et al. in press). Within Ya-

TABLE 1.—Distance of nesting birds from the mouth of Yaquina Estuary in 1979 (calculated from Pitman et al. in press).

	Cumulative number of nesting birds				
	≤7 km	≤20 km	≤25 km	≤45 km	≤50 km
common murres[1]	[2]2,800	[2]6,800	[2]6,800	[2]6,800	[3]22,000
western gulls	398	528	536	541	1,231
cormorants	418	653	1,581	1,727	3,041
pigeon guillemots	45	191	201	206	220

[1]Includes all breeding and nonbreeding adults at colony.
[2]Estimated for 1983 (USFWS, aerial survey; pers. obs.).
[3]Includes 1983 as well as 1979 estimates.

[1]Oregon Aqua-Foods, Inc., 2000 Marine Science Drive, Newport, OR 97365; present address: P.O. Box 1467, Newport, OR 97365.

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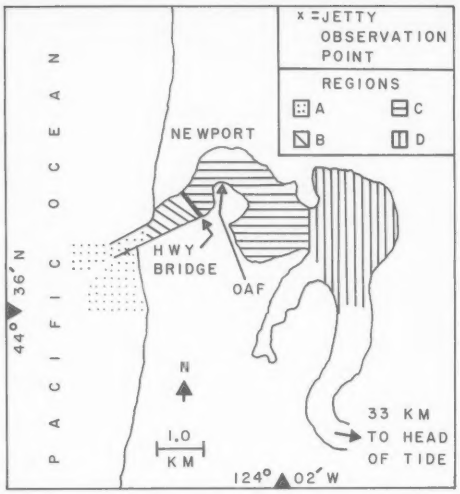

FIGURE 1.—Yaquina Estuary study regions. OAF indicates site of smolt releases.

quina Estuary, <30 pairs of western gulls (Bayer 1983) and an undetermined number of pigeon guillemots also nested in association with manmade structures. The typical nesting phenology of these birds at Yaquina Head (which is about 6.5 km north of Yaquina Estuary) has been examined by Scott (1973) and Bayer (1983) with murres beginning to fledge young in early July, gulls and pelagic cormorants in late July, and Brandt's cormorants and pigeon guillemots in early to mid-August. However, it would be invalid to assume that nesting in 1983 followed the chronologies of typical years because nesting success for cormorants and murres was abnormally low in 1983 with eggs and young being abandoned (Bayer[2]). Although the nesting success of gulls was not unusually low in 1983 (Bayer fn. 2), the chronology of their nesting might have been different than in 1982. Thus, comparing 1982 and 1983 bird numbers at Yaquina Estuary for the same stage of the nesting cycle would be tenuous. Brown pelicans, *Pelecanus occidentalis*, and Caspian terns, *Sterna caspia*, do not nest in this area.

I divided the estuary and the area around its mouth into four censusing regions (Fig. 1) with region A having an area of about 1.8 km^2; region B, 0.5 km^2; region C, 3.0 km^2; and region D, 3.2 km^2. I censused birds from observation points where I could overlook the estuary or estuary mouth with a 20× telescope when glare, heat waves, and water conditions did not obscure birds. I censused the areas around the mouth of the jetties from an observation point about halfway out on the south jetty (Fig. 1). The boundaries of region A were estimated by using the distance to the first navigation buoys to the west of the jetties as a radius that was about 1.5 km from the observation point and 1.0 km from the end of the jetties to estimate the outer boundary. All taxa except pigeon guillemots were censused during a single continuous sweep of nonoverlapping portions of a region; pigeon guillemots were enumerated during two sweeps per portion with the maximum number of the two sweeps recorded.

I censused "active" (see below) gulls and cormorants, nonflying common murres and pigeon guillemots (including guillemots standing on stationary objects), roosting Caspian terns, all brown pelicans, and all marbled murrelets, *Brachyramphus marmoratus*. "Active" gulls were those that flew over or sat in the water (gulls sitting on stationary roosts were not included). Gull species included western, glaucous-winged, *L. glaucescens*, and western × glaucous-winged gull hybrids (Hoffman et al. 1978). Cormorants present were usually either Brandt's or pelagic cormorants, but some double-crested cormorants, *P. auritus*, were also included. "Active" cormorants were those on the water surface or those making short flights in association with a feeding flock; cormorants on transit flights through a region or roosting on stationary objects were not counted. Only nonflying murres and guillemots were included because others flew through regions A and B without landing (and feeding). Although roosting Caspian terns were obviously not feeding, they were recorded because their numbers were an index of the total numbers present and because it was not possible to count foraging (i.e., flying) Caspian terns accurately. There were 166 censuses during 37 d from 1 June to 16 September 1982 at regions A-D during variable tidal conditions, and 39 censuses within 2 h of low tides before 1500 Pacific Daylight Time (PDT) during 39 d from 1 June to 30 August 1983 at regions A-C. Each census took 45-75 min, depending upon the number of birds present.

Comparisons of bird numbers between 1982 and 1983 were only made for censuses within 2 h of low tides before 1500 PDT. Comparisons were made during the 1 June to 30 August period for brown pelicans, "active" cormorants, "active" gulls, and

[2]Bayer, R. D. In prep. Breeding success of seabirds along the mid-Oregon coast concurrent with the 1983 El Nino. Unpubl. manuscr. P.O. Box 1467, Newport, OR 97365.

pigeon guillemots because the numbers of these birds during this period did not show any signs of seasonal variation. But for common murres, the periods of comparison were 1 June-31 July and 1-30 August, and the periods for Caspian terns were 1 June-10 July, 11 July-5 August, and 6-30 August. The periods for common murres and Caspian terns were chosen because in one or both years there were marked seasonal changes in bird numbers between or among these periods.

The number of days postrelease refers to the number of daylight periods after a smolt release (Myers 1980). For example, if smolts were released on Monday night or early Tuesday morning, then Tuesday after dawn would be considered as 1-d postrelease (i.e., the first day, or first daylight period, after a release).

If variances were not significantly different, then the student's *t*-test for two means or the analysis of variance (ANOVA) for three or more means were calculated to determine statistical differences between or among means. If variances were significantly different, the Mann-Whitney U test or normalized Mann-Whitney *z* test (Zar 1974, p. 109-113) for two samples or the Kruskal-Wallis rank H or H_c (if ranks were tied) test (Zar 1974, p. 139-142) for three or more samples was used. All tests were two-tailed.

RESULTS AND DISCUSSION

Smolt Releases

Oregon Aqua-Foods, Inc. (OAF) has released 2 million or more salmon smolts (almost all coho salmon, *Oncorhynchus kisutch*) each year since 1977 into Yaquina Estuary between June and August. In 1982 and 1983, the proportion that were coho salmon was 98% and 94%, respectively; the remainder were chinook salmon, *O. tshawytscha*. Until 1983, these releases were under variable tidal conditions in the evening just after dark to minimize bird predation of smolts as they were released. In 1983, salmon smolts were released either in the evening or early morning on the ebbing tide while it was still dark.

Salmon smolts do not immediately swim to the ocean after they are released. Myers (1980) found that the number of OAF smolts in the Yaquina Estuary declined exponentially after a release. During June-August releases in 1978, half the smolts left the estuary within an average of 3.9 d (SE = 0.7 d, range 1.7-9.0 d, N = 9 releases) with a few smolts remaining in the estuary several months (calculated from Myers 1980). There are no data to determine if the smolt residency time in the estuary differed between 1982 and 1983.

In 1982 and 1983 from June through August, the interval between releases averaged <2.5 d, and an average of 0.2-0.3 million fish were released each time (Table 2). Although the average release interval was longer and the number of fish per release usually greater in 1983, these differences were not significant (Table 2). But the biomass of fish per release was significantly greater in 1983 than in 1982 in the June-July and June-August periods (Table 2). Overall, 1.6 million fewer fish were released in 1983 than 1982, but the total biomass released was almost 38 metric tons (t) greater (Table 2); this resulted from smolts weighing more on the average in 1983 (32.9 g/smolt) than in 1982 (26.7 g/smolt) (calculated from Table 2).

Bird Predation of Salmon Smolts

Although all birds in this study except marbled murrelets were observed with salmon smolts in their bills, the importance of smolts in these birds' diets was not documented in this study. However, Matthews (1983) found that coho salmon smolts com-

TABLE 2.—Releases of salmon smolts in 1982 and 1983 at Yaquina Estuary. Total = total number or biomass of fish released during a period. Differences between years tested with student's *t*, Mann-Whitney U, or normalized Mann-Whitney *z* test. NS = not significant.

			Release interval (d)			No. fish/release (millions)				Fish biomass/release (t)			
Period	Year	Releases N	$\bar{x}$	SD	P	$\bar{x}$	SD	P	Total	$\bar{x}$	SD	P	Total
June-July	1982	30	2.0	1.2		0.3	0.1		9.6	7.5	2.4		225.3
	1983	25	2.4	1.7	NS	0.4	0.1	NS	9.0	11.3	4.6	<0.01	268.4
August	1982	20	1.6	0.7		0.2	0.1		4.7	7.9	3.4		158.6
	1983	12	2.4	1.6	NS	0.3	0.2	NS	3.7	12.8	9.0	NS	153.0
June-August	1982	50	1.8	1.0		0.3	0.1		14.4	7.7	2.8		383.9
	1983	37	2.4	1.6	NS	0.3	0.2	NS	12.8	11.8	6.3	<0.01	421.4

posed 13% of 287 prey items of common murres collected within 2 km of the Yaquina's jetties during the summer of 1982.

Salmon smolts appeared to be most vulnerable to predation soon after a release. When they first entered the estuary after exiting a pond through a large tube, smolts seemed disoriented and milled around the surface where they could easily be caught by birds. Night releases allowed smolts several hours to become adjusted before becoming vulnerable to predators at daylight. (The only somewhat significant nocturnal bird predator were heerman's gulls, *L. heermanni*, but they usually numbered <50 birds, were not present for every release, and were present mainly in late July and August.)

Within about 4 h after daylight after a release, some smolts were observed jumping at the mouth of the jetties in regions A and B, where birds also concentrated. For censuses of regions A-D within 2 h of low tides and within 2 d of a release in 1982, an average of 97.9% (SD = 6.3, N = 17 d) of the common murres, 91.5% (SD = 16.2, N = 17 d) of the "active" gulls, and 90.5% (SD = 26.8, N = 8 d) of the "active" cormorants censused were at regions A and B. But regions A and B accounted for only about 27% of the area of regions A-D. Evidently, the turbulent action of the estuarine water entering the ocean and/or the funneling effect of the jetties (Fig. 1) caused the smolts to be particularly vulnerable to predators there.

During the first 12 h of daylight after a release, some smolts within 0.5 km of the release site were still vulnerable to bird predation as many smolts were near the water surface. Many jumped out of the water, and some rolled on their sides exposing their silver undersides, which were highly conspicuous against the dark water background. Gulls often sat on the water and grasped a fish as it jumped into the air. Schools of smolts also milled near the surface where they were clearly visible to humans (and presumably birds).

Within-Day Variation in Bird Numbers

Bird abundance was clearly not constant within a day, and taxa did not reach maxima synchronously (Fig. 2). Censuses within 2 h of early low tides (i.e., low tides before 1500 PDT) averaged closer to the maximum number censused daily for all taxa, and censuses near high tide were usually closer to the daily maximum than counts within 2 h of evening low tides (i.e., after 1800 PDT) for all taxa except brown pelicans (Table 3). But differences in censuses among tidal conditions within a day were only significant for common murres and "active" gulls (Table 3).

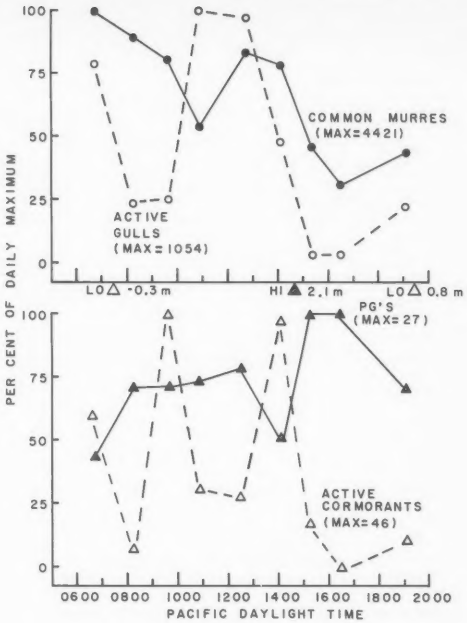

FIGURE 2.—Percentage of daily maximum number of common murres, "active" gulls, "active" cormorants, and pigeon guillemots (PG's) observed on 5 August 1982 (which was two days postrelease) at regions A-D. Times and heights of measured low (LO) and high (HI) tides are indicated by open and closed triangles, respectively. MAX = maximum number of birds seen on 5 August.

A single census at any time of day is unlikely to estimate accurately the maximum number of birds of any taxon present that day (Table 3). The average census only ranged from 10.8% to 63.7% of the daily maximum (Table 3). The best censuses to use for estimates would be those within 2 h of a morning or afternoon low tide because their averages (44-64% of daily maxima) were greater than for high and evening low tides, and their CV's (41-82%) were generally lower than for other tides (Table 3).

Daily Variation in Bird Numbers

On a day to day basis, bird numbers could often be seen to increase in the first day postrelease and then to decline (Fig. 3). However, the degree of increase was variable. Overall, murres, "active" gulls in 1983, and brown pelicans exhibited the same pat-

TABLE 3.—Percentage of daily maximum number of birds observed within 2 h of actual high tides, early low tides (i.e., time of low tide before 1500 PDT), and late low tides (i.e., time of low tide after 1800 PDT). Censuses between 6 July and 17 September 1982 at regions A-D with 9-11 censuses/d (i.e., 13-14 h period). *N* = total censuses; CV = coefficient of variation.

		Percent of daily maximum birds within 2 h of								
		High tide			Early low tide			Late low tide		
	Days	*N*	$\bar{x}$	CV (%)	*N*	$\bar{x}$	CV (%)	*N*	$\bar{x}$	CV (%)
common murres	9	31	[1]30.8	92.5	24	[1]63.7	55.3	11	[1]20.3	100.0
"active" gulls	10	35	[2]37.9	81.5	28	[2]49.5	71.9	11	[2]18.1	100.0
brown pelicans	6	21	[3]39.1	79.0	14	[3]44.0	81.8	8	[3]49.1	58.9
"active" cormorants	4	14	[4]32.6	112.6	7	[4]61.3	65.3	6	[4]10.8	142.6
pigeon guillemots	3	10	[5]52.9	58.8	8	[5]58.0	41.0	3	[5]33.9	93.8

[1]Heterogeneity, Kruskal-Wallis $H_c = 16.36$, $P < 0.01$.
[2]Heterogeneity, Kruskal-Wallis $H_c = 7.62$, $P < 0.10$.
[3]Heterogeneity, Kruskal-Wallis $H_c = 0.80$, $P > 0.10$.
[4]Heterogeneity, Kruskal-Wallis $H_c = 5.62$, $P > 0.10$.
[5]Heterogeneity, Kruskal-Wallis $H_c = 1.87$, $P > 0.10$.

tern of more birds present the first day after a release than later; this pattern, however, was significant only in 1983 (Tables 4, 5). In contrast, only "active" cormorants were more numerous the second day after a release than on the first day; however, the differences in cormorant numbers among days were only significant in 1983 (Table 5).

Numbers of pigeon guillemots and Caspian terns did not show any indication of dependence on the number of days postrelease. The differences in pigeon guillemot numbers in the 1 June-30 August period among 1, 2, and 3-6 d postrelease was insignificant (1982: $F = 0.23$, df = 2, 34; $P > 0.10$; 1983: Kruskal-Wallis $H_c = 0.61$, $P > 0.10$). Sample sizes were too small to test differences for Caspian terns in 1982, but in 1983 variation with 1, 2, and 3-6 d postrelease was insignificant in either the 1 June-14 July period (when there were few Caspian terns (Kruskal-Wallis $H_c = 2.74$, $P > 0.10$)) or the 15 July-30 August period (when they were abundant (Kruskal-Wallis $H_c = 2.74$, $P > 0.10$)).

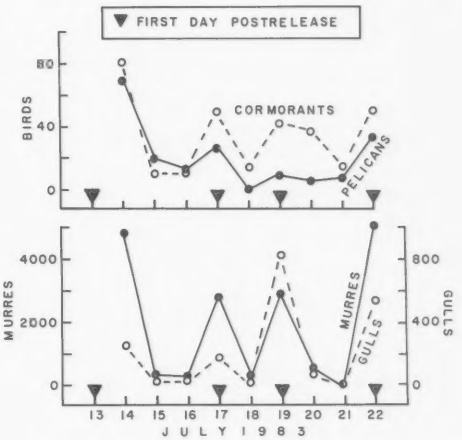

FIGURE 3.—Number of brown pelicans, "active" cormorants, "active" gulls, and common murres with relation to dates of salmon smolt releases during 14-22 July 1983 censuses that were within 2 h of low tides before 1500 PDT.

TABLE 4.—Numbers of common murres at regions A-C in 1982 and 1983 during the 1 June-31 July period when murres were abundant and the 1-30 August period when murres were infrequent in 1983. *N* = number of censuses (1 census/d within 2 h of low tides before 1500 PDT); MAX = maximum number of birds counted.

	1 June-31 July												1-30 August			
	1-d postrelease				2-d postrelease				3-6 d postrelease				1-3 d postrelease			
Year	*N*	$\bar{x}$	SD	MAX	*N*	$\bar{x}$	SD	MAX	*N*	$\bar{x}$	SD	MAX	*N*	$\bar{x}$	SD	MAX
1982	8	[1,2]3,053	967	4,310	6	[1,3]1,823	2,114	5,988	2	[1,4]1,276	824	1,858	4	[5]1,860	2,091	4,419
1983	13	[2,6]3,710	2,746	9,638	8	[3,6]2,462	2,063	6,206	6	[4,6]561	711	1,972	10	[5]106	280	901

[1]Heterogeneity among days: Kruskal-Wallis H = 4.88, $P > 0.10$.
[2]1982 vs. 1983: Mann-Whitney U = 52, $P > 0.10$.
[3]1982 vs. 1983: student's $t = 2.12$, df = 12, $P < 0.10$.
[4]1982 vs. 1983: not tested because of small sample sizes in 1982.
[5]1982 vs. 1983: Mann-Whitney U = 38, $P < 0.02$.
[6]Heterogeneity among days: Kruskal-Wallis H = 8.91, $P < 0.05$.

TABLE 5.—Comparison of bird numbers at regions A-C during 1 June-30 August period in 1982 with 1983. Day(s) = days post-release of salmon smolts, N = number of censuses (1 census/d within 2 h of low tides before 1500 PDT), and MAX = maximum number of birds counted.

		"active" gulls			brown pelicans			"active" cormorants		
	Days(s):	1	2	3-6	1	2	3-6	1	2	3-6
1982	N	10	7	2	10	7	3	9	7	3
	Birds ($\bar{x}$)	[1]391	[1]381	[1]445	[2]31	[2]11	[2]7	[3]18	[3]28	[3]47
	SD	272	294	36	36	10	10	13	41	38
	MAX	919	729	470	106	30	19	38	110	88
1983	N	20	9	9	20	9	9	20	9	9
	Birds ($\bar{x}$)	[1]400	[1]332	[1]26	[2]25	[2]17	[2]7	[3]46	[3]81	[3]21
	SD	349	450	25	19	22	8	33	90	15
	MAX	1,311	1,200	77	84	69	20	128	286	52

[1]1 d vs. 2 d vs. 3-6 d: 1982, Kruskal-Wallis H_c = 0.44, $P > 0.10$; 1983, Kruskal-Wallis H_c = 14.62, $P < 0.01$. 1982 vs. 1983: 1 d, student's t = 0.07, df = 28, $P > 0.10$; 2 d, student's t = 0.25, df = 14, $P > 0.10$.

[2]1 d vs. 2 d vs. 3-6 d: 1982, Kruskal-Wallis H_c = 2.44, $P > 0.10$; 1983, Kruskal-Wallis H_c = 8.71, $P < 0.02$. 1982 vs. 1983: 1 d, Mann-Whitney U = 107, $P > 0.10$; 2 d, Mann-Whitney U = 32.5, $P > 0.10$; 3-6 d, Mann-Whitney U = 14, $P > 0.10$.

[3]1 d vs. 2 d vs. 3-6 d: 1982, Kruskal-Wallis H_c = 1.84, $P > 0.10$; 1983, Kruskal-Wallis H_c = 6.14, $P < 0.05$. 1982 vs. 1983: 1 d, Mann-Whitney U = 142.5, $P < 0.02$; 2 d, Mann-Whitney U = 49, $P < 0.10$; 3-6 d, Mann-Whitney U = 20, $P > 0.10$.

Yearly Variation in Bird Numbers

Cormorants were significantly more abundant for 1 and 2 d postrelease in 1983 than in 1982 but not for 3-6 d postrelease (Table 5). Brown pelicans were about as numerous in 1983 as in 1982 in the 1 June-30 August period (Table 5).

Gulls were not significantly more abundant in 1983 than in 1982 in the 1 June-30 August period (Table 5), and their nesting success was also not lower in 1983 than in other years (Bayer fn. 2). But Caspian terns were significantly more abundant during the 11 July-5 August period (when many emigrated) in 1983 than in 1982 (Bayer 1984).

There were an average of about 650 more common murres per census in 1983 than in 1982 during the 1 June-31 July period for either 1 or 2 d postrelease, but the differences were only significant for 2 d postrelease (Table 4). In contrast, there were more murres in 1982 than in 1983 during this period for 3-6 d postrelease, but there were only two samples in 1982 (Table 4).

In the 1-30 August period, there were significantly fewer murres in 1983 than in 1982 (Table 4). The low numbers in 1983 resulted from the mass exodus of murres after 31 July, whereas in 1982 murre numbers did not decline as dramatically until after 12 August. In fact, there were still more murres present within 2 h of low tides on 3 and 16 September 1982 (186 and 318 murres, respectively) than in 10 censuses on different days between 1 and 18 August 1983 (i.e., ≤56 murres). The early exodus of murres in 1983 probably resulted from them migrating north early because they were unusually numerous in inland marine waters of Washington during the summer of 1983 (Mattocks et al. 1983).

During the June through August period at regions A-C, pigeon guillemot numbers were about 29% greater during 1982 ($\bar{x}$ = 23.9, SD = 11.0, N = 13 d) than in 1983 ($\bar{x}$ = 17.1, SD = 7.8, N = 35 d), a significant difference (t = 2.39, df = 46, $P < 0.05$). This decrease could have resulted from the large number of mortalities in the spring of 1983 (Hodder[3]).

Marbled murrelets were not observed in any of 120 censuses of regions A-D in the June through 20 August period of 1982. In 1983 at regions A-C, they were observed in only 1 of 21 censuses in June and August, but an average of 3.9 murrelets/census (SD = 8.7, range 0-32, N = 17 censuses) were counted in July. The difference in the number of murrelets per census in July was significantly greater in 1983 than in 1982 (normalized Mann-Whitney z = 2.18, $P < 0.05$). They were only observed at region A.

CONCLUSIONS

It is not possible to relate the number of birds nesting near the Yaquina Estuary with the number feeding there for several reasons. First, the number of nesting and nonbreeding birds is unknown, so it is not possible to determine what proportion of the birds censused were nonbreeders. Second, censuses of feeding birds represent the number of birds feeding at only one point in time, but nesting birds probably fed serially at the Yaquina Estuary (i.e., birds came and went as individuals or small flocks not as massive synchronous flocks). With serial use, the number of nesting birds using the Yaquina Estuary could be much larger than indicated by censuses. Unfortunately, birds would have to be individually recognizable to determine the degree of serial use, and this was beyond the scope of this study.

It also was not possible to tell from how far nesting birds came to feed at the Yaquina Estuary in either year because birds were not individually marked. Murres, however, may have come from long distances. In both years, the average number of murres one day after a salmon release (Table 4) was greater than the number of murres at a colony <7 km away (Table 1), and the maximum number

[3]J. Hodder, Institute of Marine Biology, Charleston, OR 97420, pers. commun., 1984.

of murres simultaneously seen at the Yaquina (Table 4) was greater than the number of murres at colonies within 45 km of the Yaquina (Table 1).

It was somewhat surprising that more cormorants and common murres were not at the Yaquina Estuary in 1983, because they then had a poor nesting season, probably as a result of a food shortage (Bayer fn. 2). There are several possible reasons why there were not more cormorants and murres counted in 1983. First, the number of salmon smolts available at the Yaquina Estuary might have been insufficient or the distance between the Yaquina and their nesting site too great for these birds to be dependent solely on salmon smolt releases. If the salmon smolt releases had been oftener and nearer to bird nesting colonies, the numbers of birds present could have been much greater. Second, there may have actually been many more birds in 1983 than in 1982, but a single census per day regime was inadequate to measure this (Table 3). Censuses throughout the day in 1983 or measurements of the serial use of the Yaquina Estuary in 1982 and 1983 might have indicated that there were dramatically more birds using the Yaquina in 1983 than in 1982. Finally, the lack of there not being a greater influx of birds in 1983 might be because many of the murres and cormorants that normally remained near the Yaquina dispersed to avoid the generally poor feeding conditions between releases. Many Oregon pelagic and Brandt's cormorants had abandoned nesting by mid-July 1983 (see Bayer fn. 2; Hodder fn. 3), and many murres may have left the Oregon coast before it became apparent at the Yaquina Estuary at the end of July. Early dispersal or migration is known for southern seabirds during an El Nino (Duffy 1983a; Schreiber and Schreiber 1984).

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DEVELOPMENT AND EVALUATION OF METHODOLOGIES FOR ASSESSING AND MONITORING THE ABUNDANCE OF WIDOW ROCKFISH, *SEBASTES ENTOMELAS*

MARK E. WILKINS[1]

ABSTRACT

Rapid expansion of a new fishery for widow rockfish, *Sebastes entomelas*, stocks off the Pacific coast of the United States began in 1979. Within 3 years, landings rose from <1,000 t to almost 30,000 t of a species for which little information on abundance or life history was available. It was known that widow rockfish occurred in irregularly distributed, dense, midwater, and semidemersal schools primarily during the night, which posed problems in directly assessing this resource. Therefore, a project was designed to further investigate the habits and distribution of the species and develop an adequate assessment methodology.

Line transect survey methods, using sector scanning sonar to estimate the number of schools per unit area and standard hydroacoustic echo integration techniques to estimate school biomass, were used in study areas off Washington and Oregon. The applicability of this methodology will depend on our ability to resolve technical problems and minimize the effects of distributional variability by refining survey design. The need for more sophisticated sonar equipment to improve data collection and processing, the extreme temporal and spatial variability of widow rockfish school size and location, and the difficulty of identifying the species composition of observed schools are matters of special concern.

The rockfish (genus *Sebastes*) of the Pacific Ocean are comprised of over 65 species exhibiting a wide array of colors, sizes, body forms, behavior, and life history characteristics. Members of this family are generally demersal or semidemersal and school over hard substrate on the continental shelf and slope. The widow rockfish, *Sebastes entomelas*, is atypical. As an adult it aggregates in dense midwater schools during the night.[2] These schools tend to disappear from established fishing grounds at dawn or shortly thereafter, becoming less vulnerable to the fishery.

The role of this species in the Pacific coast groundfish fishery changed from an undesirable incidental catch in 1978 to a major target species by 1980. Advances in fishing technology and product handling and marketing, as well as new vessels seeking alternative fisheries, promoted an increase in landings from 1,107 t in 1978 to 28,419 t in 1981 (Table 1).

By 1981, schools were becoming more difficult to locate and there was concern that the resource was being overharvested. The fishery began expanding into new areas to maintain profitable catch rates. During late 1981 and early 1982, most of the widow rockfish were being taken from the vicinities of Bodega Bay and Monterey, CA, though fishing was taking place as far north as Cape Flattery, WA.

The rapid growth of this new fishery resulted in large catches from a resource about which little was known. Research on this species prior to 1979 was limited to general descriptions of distribution, habitat, and biological characteristics (Hitz 1962; Phillips 1964; Pereyra et al. 1969). Scientists began gathering data in 1978 to determine the impact of the fishery on the condition of the stock, to define the distribution and size of the stock, and to establish a baseline of biological characteristics of the species. Commercial landings have been sampled by State

TABLE 1.—Landings of widow rockfish by state for years 1973-83 in metric tons.

Year	Washington	Oregon	California	Total
1973	81	15	29	125
1974	18	7	47	72
1975	13	11	57	81
1976	51	55	147	253
1977	277	34	267	578
1978	428	472	207	1,107
1979	1,697	1,960	636	4,293
1980	6,632	8,718	4,808	[1]20,677
1981	7,211	14,689	6,519	28,419
1982	6,030	9,262	10,270	25,562
1983	3,293	3,151	3,455	9,899

[1]This also included 519 t of joint venture and foreign catch.

[1]Northwest and Alaska Fisheries Center Seattle Laboratory, National Marine Fisheries Service, NOAA, 7600 Sand Point Way N.E., Building 4, BIN C15700, Seattle, WA 98115.

[2]Groundfish Management Team. 1981. Status of the widow rockfish fishery. Unpubl. manuscr., 41 p. Pacific Fishery Management Council, 526 S.W. Mill Street, Portland, OR 97201.

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FISHERY BULLETIN: VOL. 84, NO. 2, 1986.

and Federal agencies in Washington, Oregon, and California for information on size and age composition, sex ratio, maturity, feeding habits, morphometrics, meristics, and fecundity.

Widow rockfish abundance was estimated by the Groundfish Management Team (fn. 2, 1982[3]) of the Pacific Fisheries Management Council, using cohort and stock reduction analyses (SRA) (Kimura and Tagart 1982). These stocks were found to have been fished down from their virgin level and were thought to be approaching a biomass level which would, under prudent management, produce a maximum sustainable yield of about 12,000 t in the INPFC (International North Pacific Fisheries Commission) Columbia and Eureka areas.

Research surveys were needed to complement these analyses by providing independent estimates of abundance, describing the distribution, and collecting biological information not available from fishery data (for example, data on prerecruits and fish in areas which will not support a profitable fishery). Widow rockfish present special problems to those seeking to estimate their abundance through research surveys. The species is not usually available to bottom trawls, precluding traditional "area-swept" trawl surveys, and its tightly clustered distribution and inconsistent schooling behavior reduce the effectiveness of traditional hydroacoustic surveys.

In 1980, the Northwest and Alaska Fisheries Center (NWAFC) began developing a practicable method to survey widow rockfish stocks. Scientists needed to understand the distribution and behavior of widow rockfish to determine which survey methods might be most appropriate to measure the size of the resource. The first objective of the project, therefore, was to study aspects of the behavior, distribution, and biology of the species. The distribution of its characteristic nighttime aggregations relative to features of submarine topography was of particular interest. The distribution of this species is highly variable both on a diel basis and over longer periods, and the reasons for this variability were also of interest. Another question concerned what proportion of the total resource is present in detectable schools and how that proportion changes in space and time. Clark and Mangel (1979) described a theoretical situation in yellowfin tuna stock dynamics wherein detectable, fishable schools are constantly being replenished from an undetectable portion of the population. They discussed the implications of this behavior in a fishery. If such a phenomenon could be confirmed in widow rockfish, determining the detectable proportion of the population might enable us to estimate the absolute size of the resource.

The second objective of the project was to investigate methodologies with potential for estimating widow rockfish stock size, considering the species' behavior and distribution patterns. The final objective was to evaluate the effectiveness of the chosen technique when actually implemented.

The project was conducted in three phases: 1) an examination of the biology and behavior of widow rockfish on commercial fishing grounds, 2) the development of a practical survey method for assessing distribution and abundance, and 3) an evaluation of the feasibility and effectiveness of applying such assessment methodology to widow rockfish on a routine coastwide monitoring basis. Field studies were initiated in March 1980 and concluded in April 1982. Behavior studies were conducted during August 1980 and April 1981. Field work focusing on methodology development took place during late March 1980 and mid-March 1981, and the trial assessment survey took place during mid-March to early April 1982. All field work was conducted off Oregon and southern Washington (Fig. 1).

The purpose of this report is to document the work done to date on the development of widow rockfish assessment methodologies, to evaluate the utility of those methods for routine assessment and monitoring of widow rockfish stocks and other species exhibiting a similar behavior, and to recommend means of enhancing future assessment efforts.

BEHAVIOR STUDIES (1980-81)

The nature of the fishery made it apparent that the behavior of widow rockfish differed from that of other commercially important species of the genus *Sebastes*. Extremely large widow rockfish catches were taken by midwater trawlers operating almost exclusively at night and fishing on very dense midwater schools in only a few small areas along the coast.

The first phase of the project studied the behavior and habits of widow rockfish to determine their distribution patterns, using demersal and midwater trawls and hydroacoustic observations. This included determining where the fish go when the dense, midwater schools disperse; whether there are components of the stock other than the typical midwater aggregations; and at what period in their daily cycle

[3]Groundfish Management Team. 1982. Status of the widow rockfish fishery. Unpubl. manuscr., 22 p. Pacific Fishery Management Council, 526 S.W. Mill Street, Portland, OR 97201.

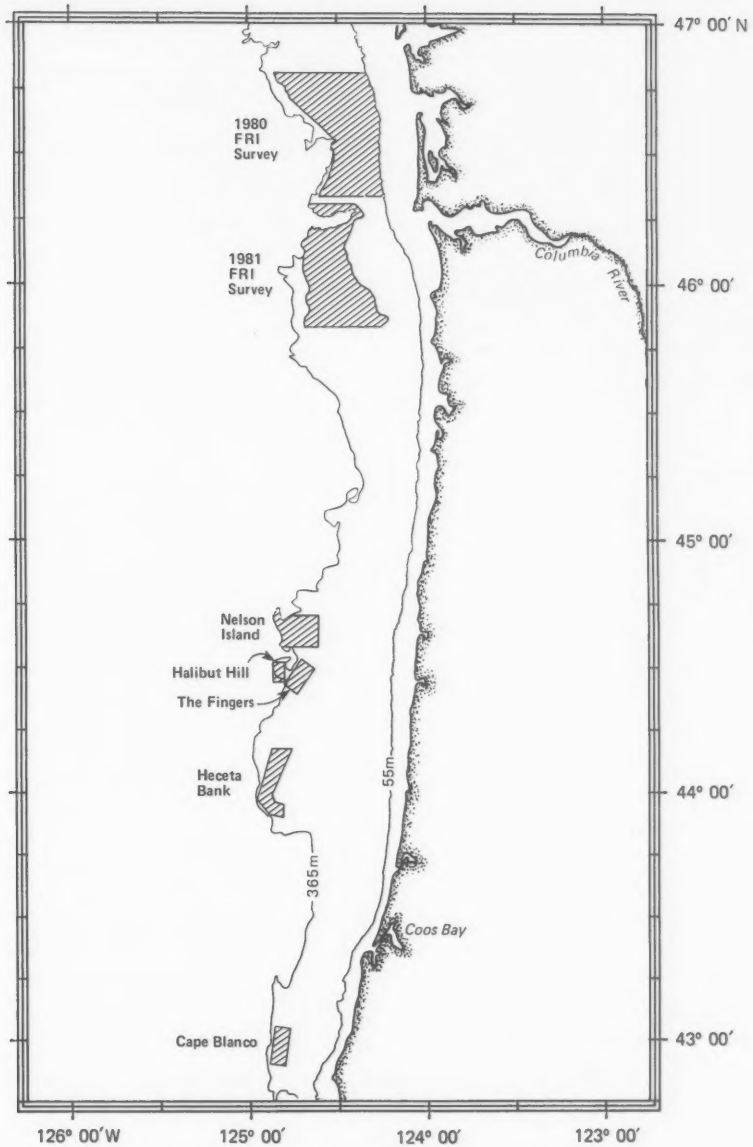


FIGURE 1.—Widow rockfish survey areas off the coasts of Washington and Oregon occupied during field work conducted between 1980 and 1982.

their availability is most stable. Other objectives were to investigate the possible causes of their diel aggregation habits and to develop an ability to distinguish widow rockfish schools from those of other species on the basis of echosign[4] characteristics and test fishing.

Methods

The behavior study was initiated 11-13 August 1980 aboard the chartered trawlers *Pat San Marie* and *Mary Lou*. Concurrently, scientists aboard the NOAA RV *Miller Freeman* conducted a conventional echo integration survey in the study area and made four midwater tows to identify the species composition of the schools sighted. The survey was repeated during 10-26 April 1981 aboard the NOAA RV *Chapman* and included 7 d of hydroacoustic and sonar observations.[5] Descriptions of the vessels, trawls, and hydroacoustic equipment employed appear in Tables 2, 3, and 4, respectively.

Demersal trawl stations were located around a seabed rise known as Nelson Island off Newport, OR, to determine if significant quantities of widow rockfish occurred on or near the bottom in an area where they were known to form dense midwater aggregations. A 4 × 4 station grid with interstation distances of 4.6 km (Fig. 2) was established between the depths of 110 and 360 m with the rise at the center. Two trawl hauls were attempted at each station: one during daylight and one during darkness. When significant midwater fish schools were observed, they were sampled with midwater trawl gear for species composition.

The contents of each trawl haul were sorted by species, weighed, counted, and recorded. Otoliths were removed from samples selected for age determination and stage of maturity was recorded for some individuals. Stomach sample collections, stratified by fish length, were also taken and preserved for feeding studies.[6] No meaningful description of age and length composition was possible because of the small catches.

Consultations with fishermen, observation trips aboard commercial trawlers, and observations during research operations provided further information about school characteristics and diel behavior patterns of widow rockfish and other species on and around widow rockfish fishing grounds.

Results

Twenty-seven demersal tows were completed during the August 1980 widow rockfish behavior study, including 12 at night and 15 during the day. The trawl was damaged during two night hauls. The widow rockfish catch was small, with 1 or 2 specimens in six hauls and 20 specimens in one of the night hauls during which the trawl was damaged (Fig. 3, 1980). Therefore, no conclusions about diel movement patterns were possible from the 1980 study.

The *Miller Freeman* transected the Nelson Island area during the same study period and found one

[4]"Echosign" can be defined as the echo return output (paper echograms, video chromoscope displays, etc.) of an echo sounder aimed at targets in the water column.

[5]Thomas, G. L., C. Rose, and D. R. Gunderson. 1981. Rockfish investigations off the Oregon coast, annual report. Unpubl. manuscr., 20 p. Univ. Wash., Fish. Res. Inst., FRI-UW-8119.

[6]Adams, P. B. 1984. The diet of widow rockfish (*Sebastes entomelas*) in northern California. Unpubl. manuscr. Southwest Fisheries Center Tiburon Laboratory, National Marine Fisheries Service, NOAA, 3150 Paradise Drive, Tiburon, CA 94920.

TABLE 2.—Vessels used during the widow rockfish assessment project.

Vessel	Length (m)	Main engine (hp)	Survey type	Agency[1]	Dates
Muir Milach	26	800	Hydroacoustic sonar	FRI	19 Mar.-2 Apr. 1980
Pat San Marie	31	765	Behavior	NWAFC	11-13 Aug. 1980
Mary Lou	26	700	Behavior	NWAFC	11-13 Aug. 1980
Miller Freeman	66	2,200	Behavior and hydroacoustic	NWAFC	11-13 Aug. 1980
Alaska	30	600	Hydroacoustic sonar	FRI	12-23 Mar. 1981
Chapman	39	1,165	Behavior and hydroacoustic sonar	NWAFC	7-26 Apr. 1981
Ocean Leader	36.5	1,125	Hydroacoustic sonar	NWAFC	14 Mar.-7 Apr. 1982

[1]FRI = Fishery Research Institute; NWAFC = Northwest and Alaska Fisheries Center.

TABLE 3.—Fishing gear used during the widow rockfish assessment project.

Trawl type	Vessels	Doors and accessory gear	Approximate fishing dimensions
Bottom trawl			
Nor'eastern	*Pat San Marie* and *Mary Lou*	1.5 × 2.1 m steel V-doors, 55 m triple dandylines, 32 mm mesh cod end liner, roller gear	9.1 m headrope height, 13.4 m wingspread
	Muir Milach and *Chapman*	Same as above but with 1.8 × 2.7 m steel V-doors 2,500 lb	6.10 m headrope height, 16.7 m wingspread (Wathne[1])
	Alaska	Same as above but with 1.6 × 2.9 m aluminum V-doors	(not measured)
Midwater trawl			
Alaska Diamond	*Chapman*	1.8 × 2.7 m steel V-doors, 55 m double dandylines with 4 sets of 5.5 m bridles, 125 kg weights attached to the bottom of each wingtip, 32 mm mesh cod end liner	11.0-14.6 m vertical opening 15.2 m wingspread
	Alaska	Same as above but with 1.6 × 2.9 m aluminum V-doors	Same as above
Norsenet	*Miller Freeman*	6 m^2 Waco doors, 75 m double dandylines, 46 mm mesh cod end covered with a double braided 144 mm mesh bag	18-20 m vertical opening
No. 7 Gourock rope wing	*Muir Milach*	4.6 m^2 Suberkrub doors, 73.2 m double dandylines, 114 mm mesh cod end (no liner)	18.3 m vertical opening, wingspread not measured
No. 8 Gourock rope wing	*Ocean Leader*	4.5 m^2 Suberkrub doors, 100 m dandylines 200 kg weights attached to the bottom of each wing, 32 mm mesh cod end liner	21.3 m vertical opening, wingspread not measured

[1]Wathne, F., Northwest and Alaska Fisheries Center, 2725 Montlake Blvd. E., Seattle, WA 98115, pers. commun. June 1981.

TABLE 4.—Hydroacoustic equipment used during widow rockfish behavior and assessment surveys, 1980-82. FRI = Fisheries Research Institute; NWAFC = Northwest and Alaska Fisheries Center.

Vessel:	*Muir Milach* (FRI)	*Miller Freeman* (NWAFC)	*Alaska* (FRI)	*Chapman* (NWAFC)	*Ocean Leader* (NWAFC)
Dates used	19 March-2 April 1980	11-13 August 1980	12-23 March 1981	21-26 April 1981	14 March-7 April 1982
Echo sounder and transducer	Simrad[1] EK-38 11° beam at −3dB	Simrad EK-38 12° beam at −3dB	Simrad EK-38 11° beam at −3dB	Simrad EK-38 11° beam at −3dB	Biosonics 101 7° beam at −3dB
Towed V-fin transducer housing	2-ft Braincon	2-ft Braincon	2-ft Braincon	2-ft Braincon	2-ft Braincon
Tape recorder	TEAC 3440A reel-to-reel	cassette	TEAC 3440A reel-to-reel	TEAC 3440A reel-to-reel	cassette
Chart recorder	Simrad wet paper	Simrad dry paper	Simrad wet paper	Simrad wet paper	EPC 1600 dry paper
Portable echo integrator	Biosonics 120	NWAFC acoustic research container system	Biosonics 120	Biosonics 120	Biosonics 120
Computer	Not used	NWAFC acoustic research container system	Not used	Not used	Radio Shack TRS-80
Sonar system	C-Tech LSS-68 68 kHz sector scanning	Not used	C-Tech LSS-68 68 kHz sector scanning	Simrad SQ searchlight beam	Furuno FSS-75 75 kHz sector scanning
Video camera and recorder	RCA C004 camera Panasonic recorder	Not used	RCA C004 camera Panasonic recorder	RCA C004 camera Panasonic recorder	RCA C004 camera Panasonic recorder

[1]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

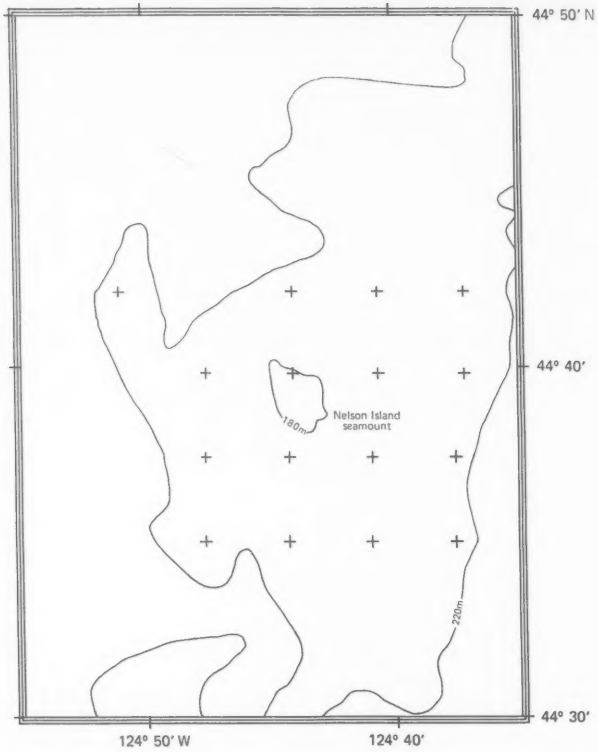


FIGURE 2.—The demersal trawl station grid occupied during 1980 and 1981 widow rockfish behavior studies on the Nelson Island ground off Newport, OR. The 16 trawl stations are marked with a (+).

school of widow rockfish, which was sampled with midwater trawl gear (Fig. 4). It was not possible to stay in contact with the school long enough to observe diel changes in behavior.

When the study was repeated in April 1981, only 4 of 20 demersal tows contained widow rockfish. Two of these tows contained only a single specimen each, while the others contained 20 and 28 specimens. Results again indicated that widow rockfish were relatively unavailable to demersal trawl gear and that their distribution was somewhat more closely associated with Nelson Island during the night than during the day (Fig. 3, 1981).

It is important to be able to distinguish widow rockfish from other species on the basis of echosign in order to draw conclusions about their behavior, distribution, and abundance. Commercial fishermen targeting on this species have shown that this can be done. We characterized the echosign produced by widow rockfish and other species occurring on widow rockfish grounds using echograms obtained aboard research and commercial vessels and through discussions with commercial fishermen on echograms and corresponding catches. Widow rockfish schools most frequently appeared on echograms as tall, slender columns suspended over an irregular bottom (Fig. 5). These were often accompanied by less dense layers probably composed of salps and other zooplankton. Widow rockfish were sometimes present during evening and morning in smaller schools high in the water column (Fig. 6). Shortbelly rockfish, *Sebastes jordani*, and redstripe rockfish, *S. proriger*, have similar echosign characteristics and are most likely to be confused with widow rockfish off the Oregon coast (Figs. 7, 8). Other midwater targets in the area were identified as layered schools of

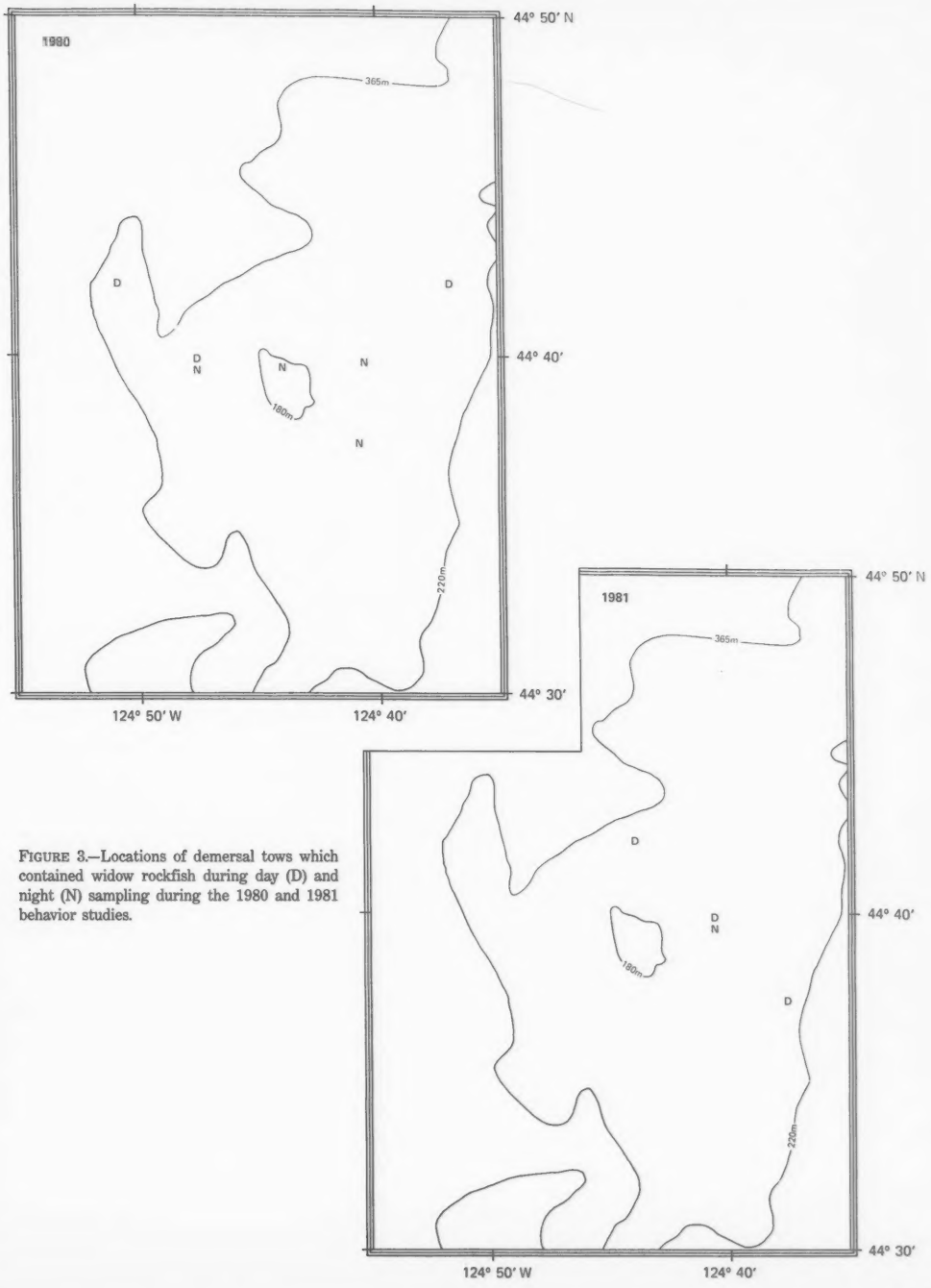


FIGURE 3.—Locations of demersal tows which contained widow rockfish during day (D) and night (N) sampling during the 1980 and 1981 behavior studies.

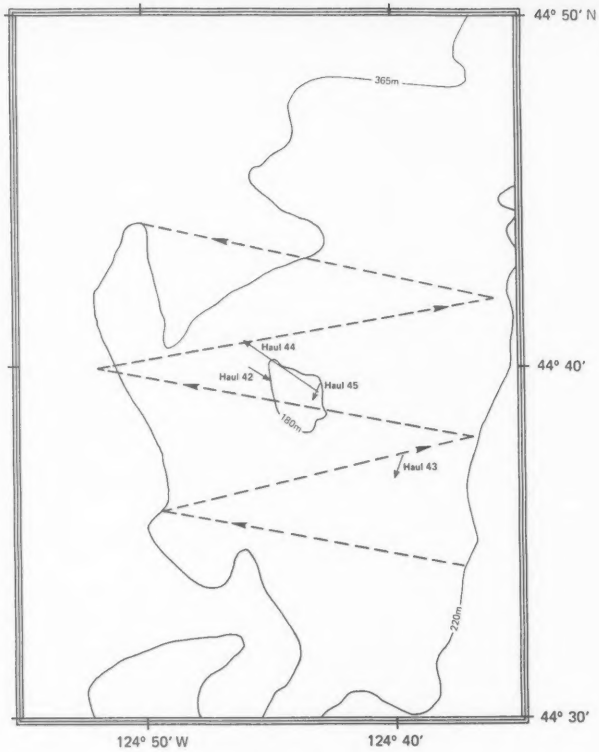


FIGURE 4.—Hydroacoustic transects (dashed lines) and midwater trawl hauls (solid arrows) conducted by the RV *Miller Freeman* during the 1980 behavior study. Only haul 43 contained widow rockfish (1,247 kg).

Pacific whiting, *Merluccius productus*, (Fig. 8) or less dense layers of zooplankton.

The formation and dispersal of widow rockfish aggregations was observed during the research cruises. During a typical night, small schools would appear in late evening (from 2000 to 2400) either near bottom or high in the water column. As the night progressed, these schools tended to grow and those high in the water would settle toward the bottom. Peak school size and density usually occurred between 0200 and dawn. Shortly after daybreak, most schools would separate into smaller schools and rise off the bottom. The schools would sometimes move over deeper water while maintaining their nighttime configuration.

Departures from the typical behavior patterns have been reported. For example, while observing widow rockfish schools over the continental shelf (not aggregating around a seamount), Gunderson et al.[7] noted a progressive offshore shift in the location of the schools during one night. By sunrise most of the schools were located near the edge of the shelf. Most of these schools dispersed after dawn, but some remained on the bottom in the area (in one case as late as 1037 when observations were terminated). This apparent shift may have been related to diurnal vertical migration behavior (Pereyra et al. 1969).

METHODOLOGY DEVELOPMENT (1980-81)

The methodology development was conducted by

[7]Gunderson, D. R., G. L. Thomas, P. Cullenberg, and R. E. Thorne. 1981. Rockfish investigations off the coast of Washington and Oregon. Final report. Unpubl. manuscr., 45 p. Univ. Wash., Fish. Res. Inst., FRI-UW-8125.

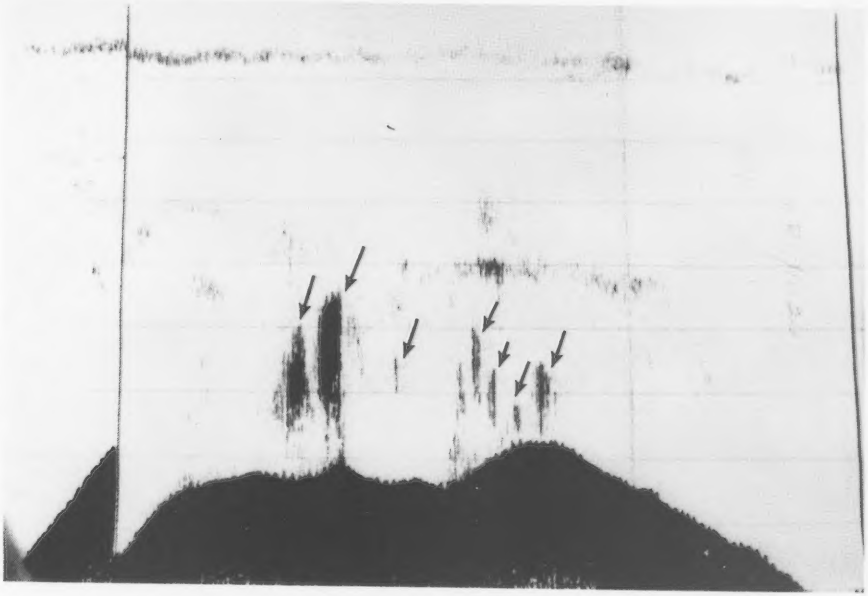


FIGURE 5.—Echogram showing the typical configuration of widow rockfish schools at night (arrows).

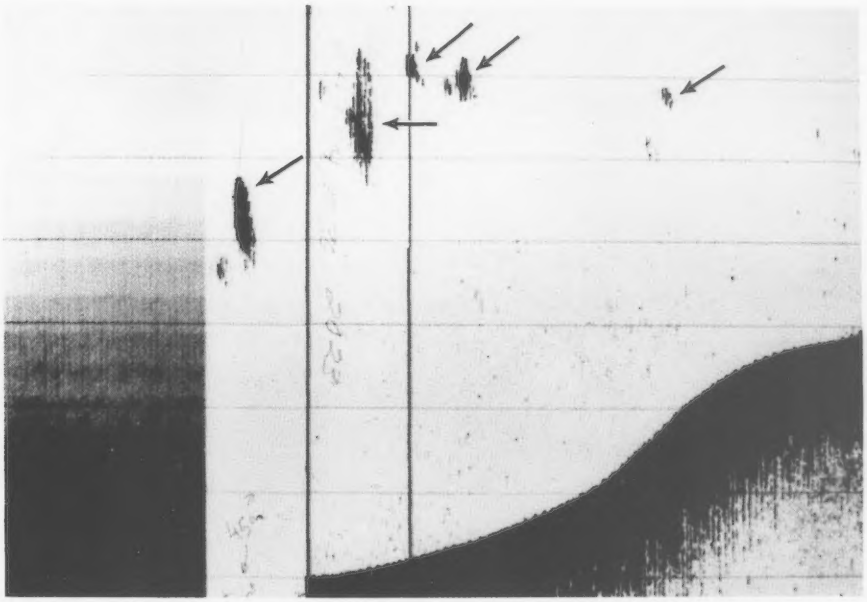


FIGURE 6.—Echogram showing the configuration of "evening and morning" widow rockfish schools (arrows).

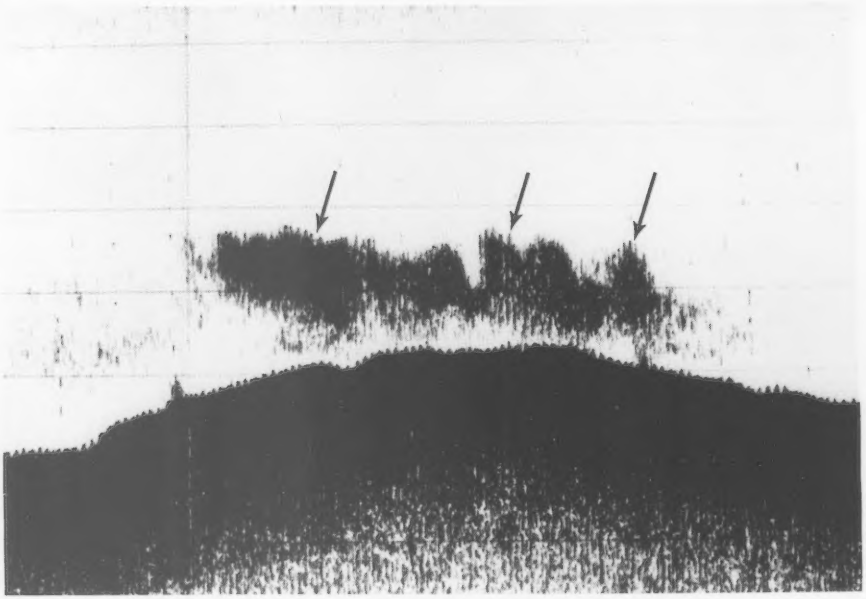


FIGURE 7.—Echogram showing the typical configuration of shortbelly rockfish schools (arrows).

FIGURE 8.—Echogram showing configuration of Pacific whiting (W), redstripe rockfish (R), and shortbelly rockfish (S) schools.

the University of Washington's Fishery Research Institute (FRI) under contract with the NWAFC (Gunderson et al. fn. 7, 8). The objectives of the work were to evaluate the applicability of several resource assessment techniques and refine the most promising approaches. In particular, it involved a comparison of three methods of quantifying widow rockfish abundance in small areas off southern Washington and northern Oregon: conventional echo integration, line transect survey theory (Burnham et al. 1980; Seber 1980), and line intercept survey theory (Seber 1973, 1980).

Methods

This study involved three research cruises off southern Washington and northern Oregon. Tables 2-4 present the dates of these cruises and specifications of the vessels, fishing gear, and hydroacoustic equipment employed. The field work entailed systematically transecting the survey areas, simultaneously recording data from quantitative echo integration equipment and sector scanning sonar. Data were collected on the number of fish schools, their perpendicular distance from the transect, their depth below sea surface, the size and density of selected schools, and the distribution of schools in relation to various features of submarine topography. The echo integration system was used in a conventional manner to obtain a measure of the density of fish within a relatively narrow acoustic beam of 10°-11° directly below the vessel (Fig. 9). Sector scanning sonar cannot measure fish density, but by employing an array of transducers radiating an acoustic signal over a 200° × 9° semicircular wedge perpendicular to the path of the vessel (Fig. 9), it can be used to count schools within about 100-200 m to each side of the vessel, measure their dimensions, and determine their perpendicular distance from the transect. The sonar's transducer array was aimed straight downward for these studies. The entire wedge was

[8]Gunderson, D. R., G. L. Thomas, P. Cullenberg, D. M. Eggers, and R. E. Thorne. 1980. Rockfish investigations off the coast of Washington. Annual report. Unpubl. manuscr., 68 p. Univ. Wash., Fish. Res. Inst., FRI-UW-8021.

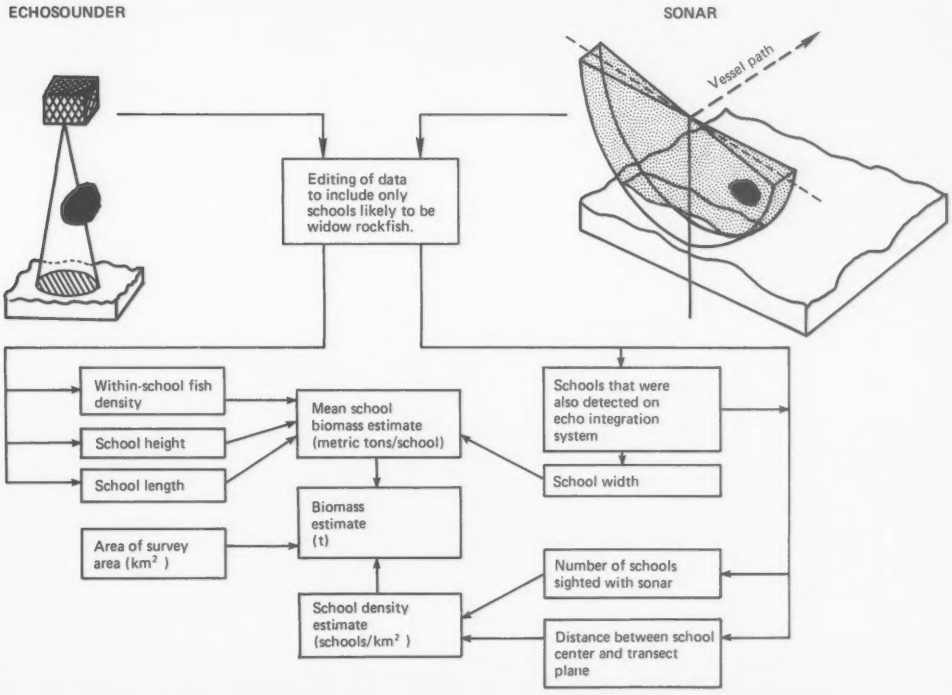

ECHOSOUNDER
SONAR
Vessel path
Editing of data to include only schools likely to be widow rockfish.
Within-school fish density
School height
School length
Mean school biomass estimate (metric tons/school)
Schools that were also detected on echo integration system
School width
Biomass estimate (t)
Area of survey area (km²)
Number of schools sighted with sonar
School density estimate (schools/km²)
Distance between school center and transect plane

FIGURE 9.—Schematic diagram depicting the analysis of echo sounder and sonar data collected during hydroacoustic line transect surveys.

displayed simultaneously on a 10-in diameter cathode ray tube (CRT) screen which provided information on the location and size of fish schools within its 200-400 m wide path (Fig. 10).

Data was collected electronically during the echo integration and sonar surveys. Echo sounder return signals were processed by an echo integrator capable of measuring voltages in variable-sized depth intervals. The echo integrator produced periodic printouts of summed integrated voltage values which corresponded to relative fish densities along the transect in various depth intervals. Analog data (receiver output voltages) were recorded onto magnetic tape as a back-up procedure and for further processing. The sonar CRT display screen was video-taped for playback and data reduction in the NWAFC laboratory.

Survey design of the 1980 and 1981 FRI studies off southern Washington was generally similar, though some aspects differed. In 1980, preselected tracklines were run and were between lat. 46°20′N and 46°48′N and between 55 and 183 m isobaths at intervals of of 3.7 km. When a significant aggregation of fish was encountered, its bounds were determined by making several mapping runs perpendicular to the main trackline. Trawling followed to determine the species composition of the aggregation and to collect biological samples. Most of the 1980 work was done during daylight with the intent of mapping and measuring yellowtail rockfish, *Sebastes flavidus*, schools. After encountering numerous widow rockfish schools at night, it became apparent that this species' schooling behavior was better suited for evaluating this methodology. Thereafter, three nights were spent transecting a smaller "widow rockfish subarea". Diel behavior and distribution were examined by making several repetitions of three selected tracklines. Near the end of this cruise an area occupied by a dense aggregation of widow rockfish schools was encountered. A short nonrandom transect was run to obtain comparable line intercept and line transect results.

In 1981, tracklines spaced every 3.7 km were transected between the depths of 128 and 220 m off northern Oregon between lat. 45°50′N and 46°18′N.

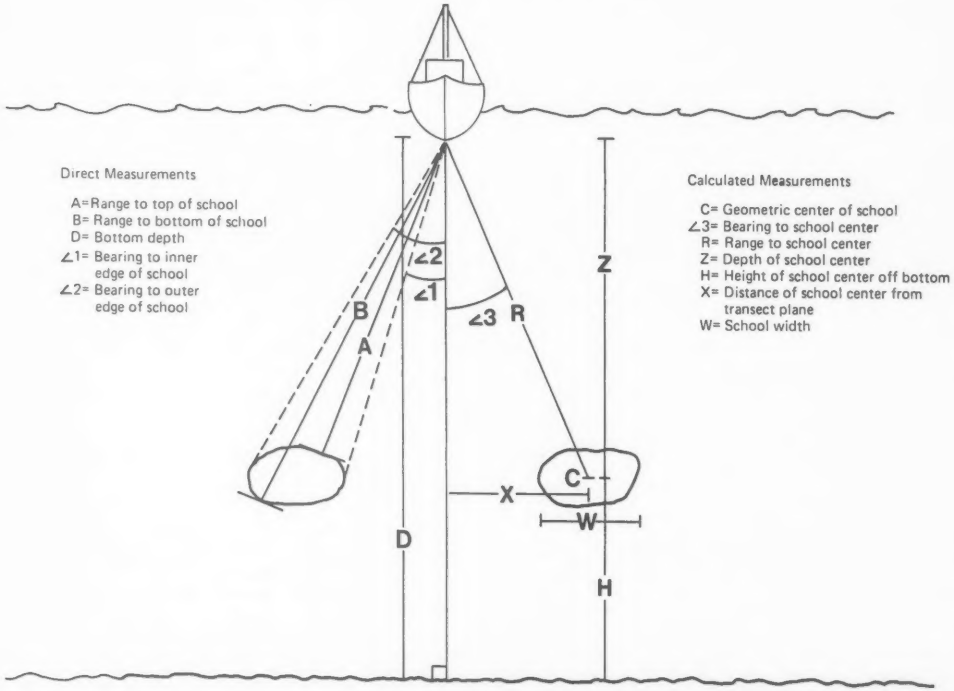


FIGURE 10.—Measurements and calculated dimensions of fish schools from videotaped sonar records.

The same procedures were used as in 1980 except that nearly all operations were conducted after dark and no mapping runs were made to define the bounds of school groups. A diel variability study was conducted on 20 March 1981 between the hours of 0153 and 1037, consisting of 13 replicates of trackline 21.

The conventional analysis of echo sounder data (integration) is based on the principle that the acoustic intensity of a signal reflected from fish targets is proportional to the density of fish in the region irradiated by the echo sounder. Detailed descriptions of the technique can be found in Moose and Ehrenberg (1971), Forbes and Naaken (1972), and Thorne (1977). During the 1980 and 1981 surveys, density estimates from this method were obtained by averaging returning acoustic signals over a series of transmissions (25 transmissions over 12.5 s during the *Muir Milach* cruise and 40 transmissions over 50 s during the *Alaska* and *Chapman* cruises). These averages were then converted from relative to absolute densities (kg/m^2) for various depth intervals using calibration data and a scaling factor based on an average target strength of −35 dB/kg.[9] Absolute abundance (biomass) was estimated by extrapolating absolute density estimates to the survey area.

Each survey area was systematically transected using the echo sounder and sonar to search for fish schools and, thereby, to derive line intercept and line transect estimates of school abundance (schools/km^2). Data on school dimensions and density were collected from those schools sighted. With the line intercept method, only the presence of a school (as detected by the echo sounder) and its width were used to estimate school abundance. This technique is based on the theory that, for systematically located transects, the probability of intersecting school i equals w_i/W, where w_i is the width of school i and W is the distance between adjacent transects. The number of schools per unit area (D) can then be estimated by

$$\hat{D} = \sum_{j=1}^{n} \frac{1}{w_j L} \qquad \text{(Seber 1980)}$$

where n = number of schools measured on a transect of length L
w_j = width of j^{th} school.

[9]The target strength value used in these analyses (−35 db/kg) was not derived during work on widow rockfish. Since accurate target strength estimation was not necessary for evaluating the utility of the methodology, we used a value which had been estimated for Pacific whiting (Dark et al. 1980) which has a similar scattering cross section.

The line intercept method was applied only to data collected from the nonrandom run made on the night of 27-28 March 1980. The data from this line were subdivided into two artificial transects of unequal length and the jackknife method (Seber 1980) was used to estimate D and its variance. This technique is described fully by Gunderson et al. (fn. 8).

Line transect theory is based on the premise that the probability of sighting a given object (or school) is a function of its perpendicular distance from the transect. A "detection function" is derived from school sighting data which relates the probability of a school being sighted to its distance from the transect. This function is used to expand the number of schools actually sighted to obtain an estimate of school abundance. The advantage of this method is that not all schools within sighting range need to be detected in order to estimate the number of schools in the area.

Using line transect estimation, the school abundance (schools per unit area) was estimated by

$$\hat{D} = \frac{n\hat{f}(0)}{2L}$$

where $\hat{D}$ = estimated number of schools per unit area
n = number of schools sighted
L = length of transect
$\hat{f}(0)$ = "detection function"—a parameter estimated from probability function for the perpendicular distances off transect of schools sighted.

The assumptions necessary for the use of this method are

1) Schools directly on the transect plane will always be sighted.
2) Schools are sighted in the position they occupied prior to the approach of the vessel, i.e. there is no avoidance of or attraction to the vessel.
3) Perpendicular distances off transect are measured precisely, particularly near the transect plane.
4) The detection function remains constant.

The computer program TRANSECT (Laake et al. 1979) was used to estimate the probability density function of the perpendicular distance of schools from the transect. The estimator model used is based on a nonparametric Fourier series expansion fit to data sets of observed perpendicular distances of

schools off the transect plane. Quinn (1979) and Burnham et al. (1980) showed that this model is robust and flexible and provides the best fit to the detection function in most applications. This estimator, at zero distance, is

$$\hat{f}(0) = \frac{1}{w^*} + \sum_{k=1}^{m} \hat{a}_k$$

where w^* = truncation width, or the effective limit of the range of detection, beyond which all observations are discarded and

$$\hat{a}_k = \frac{2}{nw^*}\left[\sum_{i=1}^{n} \cos\left(\frac{k\pi x_i}{w^*}\right)\right] \text{ (Burnham et al. 1980)}$$

where n = number of schools observed
x_i = perpendicular distance off transect for the i^{th} school
k = term number = 1,2,3,. . . m [The number of terms (m) is determined by a stopping rule in the computer program TRANSECT].

TRANSECT also computes the school abundance estimate $\hat{D}$ and its variance which is estimated by the equation:

$$\text{vâr}(\hat{D}) = (\hat{D})^2 \left[\frac{\text{vâr}(n)}{n^2} + \frac{\text{vâr}[\hat{f}(0)]}{[\hat{f}(0)]^2}\right].$$

Mean school biomass estimates were derived from density information (from echo sounder data), school dimension information (from sonar data), and an assumed target strength of −35 dB/kg. These estimates were used in the line transect and line intercept analyses. All information on schools detected by the hydroacoustic systems was edited to discriminate widow rockfish from other species using judgments based on school form, density, location, and test trawl records. Data on each school identified as widow rockfish were then integrated to obtain mean within-school density. The CRT display of the sector scanning sonar provided representations of the size, shape, and position of fish schools within its range of detection. The dimensions of all schools identified as widow rockfish were measured on the screen of a video monitor using the slow motion and freezeframe features of the video recorder-player. Dimensions measured directly included depth of school from the surface, distance off bottom, width, thickness, radial distance from vessel, and bearing to the right or left of a vertical line below the vessel (Fig. 10). The perpendicular distance of the school from the vertical plane of the vessel's path ("distance off transect") was calculated from the radial distance and bearing. All distances were measured or calculated to the apparent geometric center of each school (Burnham et al. 1980). The length of each school was calculated from the product of vessel speed and the duration that the school was being detected by the sonar, and was corrected to account for the variable sonar beam width parallel to the vessel's path due to depth.

The biomass of individual schools was estimated by the formula

$$\hat{b}_i = t_i\, l_i\, w_i\, d_i$$

where $\hat{b}_i$ = estimated biomass of school i
t_i = average thickness of school i, top to bottom (echo sounder data)
l_i = length of school i, parallel to transect (sonar data)
w_i = average width of school i perpendicular to transect plane (sonar data)
d_i = mean integration density for school i (g/m^3) assuming a target strength of −35 dB/kg (see footnote 9) (echo sounder data).

The mean school biomass (MSB) was estimated from the individual school biomass estimates; its variance was determined from

$$\text{vâr}(\hat{MSB}) = \sum_{i=1}^{N} \frac{(\hat{b}_i - \hat{MSB})^2}{N(N-1)}$$

where N = number of schools averaged for MSB.

Total biomass estimates from the line transect and line intercept methods were calculated for each survey area using the formula

$$\hat{B} = A\,\hat{D}\,(\hat{MSB})$$

where $\hat{B}$ = estimated total biomass for the survey area, and
A = total area (km^2) of the survey area.

The variance of these estimates was determined from

$$\text{vâr } \hat{B} = A^2 [(\hat{D})^2 \text{ vâr}(M\hat{S}B) + (M\hat{S}B)^2 \text{ vâr}(\hat{D}) - \text{vâr } (M\hat{S}B) \text{ vâr } (\hat{D})] \quad \text{(Goodman) 1960)}$$

Results

Twenty one trawl hauls were made during the 1980 FRI survey aboard the *Muir Milach*; 6 with bottom gear and 15 with midwater gear. Widow rockfish were caught only in midwater hauls and comprised 99% of those catches. The most abundant species in the bottom tows were spiny dogfish, *Squalus acanthias*, and black rockfish, *Sebastes melanops*. The acoustic survey consisted of 22 systematic transects covering about 550 km and employed sonar and echo integration equipment. Twenty six schools were sighted and measured to provide data for a line transect estimate of school abundance. During the nonrandom transect run on the night of 27-28 March 1980, 73 schools were sighted and measured for use in developing line transect and line intercept estimates of school abundance in a small subarea.

Only four trawl hauls were attempted during the 1981 FRI survey due to severe gear damage. Redstripe rockfish, *Sebastes proriger*, comprised 90% or more of the two catches which contained fish (one midwater haul and one bottom haul). The midwater haul was made quite close to bottom near midnight and contained small quantities of sharpchin rockfish, *Sebastes zacentrus*; widow rockfish; and greenstriped rockfish, *S. elongatus*, suggesting an association of these species in nearbottom schools at night. Fifteen systematic transects were covered during this survey (about 400 km) during which 49 schools were sighted and measured. One of the transects was replicated 13 times during one night to observe the behavior of a group of schools over the continental shelf just south of the Columbia River. These schools were not gathered around a prominent bottom feature. As the night progressed they moved deeper and further offshore, reaching the shelf break about sunrise. After sunrise most of the schools dispersed, though some remained on bottom at least until observations ceased at 1037 (Gunderson et al. fn. 7).

During the 1981 NMFS cruise, quantitative hydroacoustic data were collected from 21 transects on the Nelson Island, The Fingers, Heceta Bank, and Cape Blanco grounds (Fig. 1, Table 5) using echo integration (Thomas et al. fn. 5). The searchlight-beam sonar available on the *Chapman* was inadequate to identify school types or provide estimates of school density. This is because it employed only a single transducer programmed to sweep back and forth and did not provide continuous coverage of the area within its range. Therefore, all density and biomass figures for this survey refer to total nekton rather than widow rockfish.

TABLE 5.—The mean fish and nekton density (g/m^2) and biomass (metric tons) by location, date, and transect estimated by a conventional echo integration survey performed aboard the NOAA RV *Chapman*, 21-26 April 1981.[1]

Location	Date	Transect	Transect length (km)	Density	Mean density $\hat{D}$	Vâr $\hat{D}$	Area (km^2)	Biomass $\hat{B}$	Vâr $\hat{B}$
Crater	4/21	1	18.56	1.78					
	4/22	2	17.11	5.86	2.82	2.45	228.87	646	1.28×10^5
	4/22	3	15.02	0.66					
Cape Blanco	4/23	4	4.19	16.17					
	4/23	5	4.35	26.22					
	4/23	6	4.67	4.50					
	4/23	7	5.32	1.12	6.47	11.31	200.81	1,301	4.56×10^5
	4/23	8	6.11	1.79					
	4/24	9	2.44	1.63					
	4/24	10	3.87	0.34					
	4/24	11	3.87	0.06					
Heceta Bank	4/24	12	17.59	4.67					
	4/25	13	18.37	0.12	4.89	9.44	87.15	427	7.17×10^4
	4/25	14	15.30	10.88					
The Fingers	4/25	15	14.74	1.78					
	4/25	16	14.74	1.01	1.73	0.19	75.11	130	1.07×10^3
	4/25	17	12.22	2.54					
Crater	4/26	18	5.57	0.00					
	4/26	19	6.96	0.00	1.79	2.83	34.78	62	3.43×10^3
	4/26	20	6.28	6.75					
	4/26	21	5.63	0.26					

[1]Thomas, G. L., C. Rose, and D. R. Gunderson. 1981. Rockfish investigations off the Oregon coast, annual report. Unpubl. manuscr., 20 p. Univ. Wash., Fish. Res. Inst. FRI-UW-8119.

The results of echo integration, line intercept, and line transect analyses were compared using data collected during the 1980 and 1981 FRI cruises (Gunderson et al. fn. 7, 8). Large differences were seen between echo integration and line transect estimates in a situation where schools were relatively small and scarce (1980 transect data, Table 6). The principal reason for this is that the threshold echo voltage required to trigger the sonar CRT display was higher than that needed to detect a school on the echo integration system, so many of the sparser schools detected by the echo sounder were not detected with the sonar. In situations where schools were larger and more plentiful (1980 nonrandom runs and 1981 transects) all three methods produced similar estimates. The precision of abundance estimates generated by line transect and line intercept methods is usually comparable to that of conventional echo integration methods and can exceed it in some cases (Gunderson et al. fn. 7). The major factors which led us to concentrate our efforts on line transect surveys were the ability to cover large areas rapidly and the ability to expand the number of schools sighted by a detection function, yielding more accurate estimates of school abundance.

APPLICATION OF ASSESSMENT METHODOLOGY

By 1982 the aforementioned studies had provided a foundation of information on which to expand developmental research. The behavioral observations suggested that widow rockfish aggregations were most stable and susceptible to assessment during the night. Line transect estimation of school abundance through the use of sonar and echo integration equipment was found to be the most effective of the techniques compared, especially when school abundance was likely to be low. The next step in the project was to evaluate the feasibility of applying the line transect survey method in a comprehensive survey to assess and monitor widow rockfish stocks.

Methods

The trawler *Ocean Leader* was chartered to survey five areas off Oregon (Fig. 1) where widow rockfish had been caught consistently between 1980 and 1982. Specifications of the vessel, fishing gear, and hydroacoustic equipment used appear in Tables 2-4. The proximity of alternative grounds was important for the success of the survey, should widow rockfish not be found in one or more of the areas. At each of the grounds the survey procedure was as follows:

1) The ground was systematically surveyed with hydroacoustic equipment during the night to determine whether fish schools were in the area. The locations of schools suspected to be composed of widow rockfish, or species likely to be confused with widow rockfish, were noted. The final boundaries of the study area were then delineated.
2) The study area was surveyed at night along parallel tracklines about 1 km apart using the line transect survey technique. The tracklines were replicated as many times as practical throughout

TABLE 6.—Summary of estimates of school abundance ($\hat{D}$), mean school biomass ($\hat{MSB}$), and total biomass ($\hat{B}$) for widow rockfish. Coefficients of variation (*CV*) are given for each estimate.[1]

	$\hat{D}$ (schools/nm^2)	*CV*	$\hat{MSB}$ (t)	No. of schools	*CV*	$\hat{B}$ (t)	*CV*
1980							
Transect data							
26 schools, 2 transects							
Line transect estimate	69.5	0.84	0.12	15	0.20	204	0.84
Echo integration estimate						778	0.16
Nonrandom run data							
73 schools, 1 transect							
Line transect estimate	242.2	0.19	0.85	16	0.50	5,003	0.53
Line intercept estimate	248.9	0.10	0.85	16	0.50	5,139	0.51
Echo integration estimate						6,453	—
1981							
Transect data							
29 schools, 3 transects							
Line transect estimate	12.1	0.24	0.62	27	0.33	342	0.40
Echo integration estimate						342	0.77

[1]Gunderson, D. R., G. L. Thomas, P. Cullenberg, and R. E. Thorne. 1981. Rockfish investigations off the coast of Washington and Oregon. Final report. Unpubl. manuscr., 45 p. Univ. Wash., Fish. Res. Inst. FRI-UW-8125.

the night to provide information on variability of abundance and distribution within a given night. Selected study areas were again surveyed after an interlude of several days to study variability over longer periods.

3) Fish aggregations noted during transecting were sampled with midwater trawls for species identification. This was done on alternate nights so as not to impede the progress of the acoustic assessment portion of the survey. Biological data (e.g., size composition, maturity, stomach contents) were collected from widow rockfish in the catches.

Results

About 725 km of transects were covered in the five study areas during the 12 nights of hydroacoustic data collection. Ten midwater trawl hauls were made to identify species present in various schools. Widow rockfish schools were seen in all areas, but were sparse on the Cape Blanco, Heceta Bank, and The Fingers grounds. The Halibut Hill ground, only recently exploited, contained the highest density of widow rockfish schools and also the largest average school size. After editing videotaped sonar records, 127 schools were identified as widow rockfish; data from 37 of these were integrated on the echo sounder system and used to calculate school biomass estimates. Ideally, a mean school biomass would have been derived for each ground, but because few schools were observed there, school biomass estimates were pooled and averaged for the Nelson Island, The Fingers, and Heceta Bank grounds. No measurable widow rockfish schools were seen during surveys of the Cape Blanco ground. School abundance was estimated for each area by treating each pass through the area as a replicate and pooling data from all replicates within the area. School abundance (excepting Cape Blanco) ranged from 0.6035 schools/km^2 on The Fingers ground to 1.4810 schools/km^2 on the Halibut Hill ground. Area biomass estimates are summarized in Table 7. The total estimated biomass for the five survey areas was about 830 t; 50% at Halibut Hill ground, 30% at Heceta Bank, 11% at The Fingers, and 9% at Nelson Island.

Sampling was concentrated on the Halibut Hill ground, where widow rockfish schools were largest and most plentiful, in order to investigate the diel and night-to-night variability in school abundance. The survey of this ground was repeated seven times; three times each night on 26-27 March and 31 March-1 April and once on 30 March. Separate sighting functions for each night were estimated by pooling observations. Corresponding school abundance and mean school biomass estimates were then calculated for each night. School abundance ranged from 0.39 schools/km^2 on 26-27 March to 4.50 schools/km^2 on 30 March. Mean school biomass tended to decline as school abundance increased, however, so biomass estimates for each of the sampling periods changed less than either school abundance or mean school biomass (Table 8). It was not possible to analyze the Halibut Hill data on a replicate-by-replicate basis because few schools were sighted during any single replicate. The number of sightings per replicate ranged from 4 to 34. Burnham et al. (1980) cautioned that such stratification procedures for line transect surveys should be "severely limited to those few surveys where the number of objects seen on replicate lines is fairly large (perhaps at least in the 20 to 30 range)".

TABLE 7—Summary of estimates of school abundance ($\hat{D}$), mean school biomass ($\widehat{MSB}$), and biomass ($\hat{B}$) in each of four study areas covered during the 1982 widow rockfish assessment feasibility survey.

Study area	$\hat{D}$ (schools/km^2)	$\widehat{Var}(\hat{D})$	$\widehat{MSB}$ (t/school)	$\widehat{Var}(\widehat{MSB})$	Area (km^2)	$\hat{B}$ (t)	$\widehat{Var}(\hat{B})$	$CV(\hat{B}) = [\widehat{Var}(\hat{B})]^{1/2}/\hat{B}$
Heceta Bank	0.9490	0.0305	1.968 (6 schools)	0.656	68.60	245.76	6,758.37	0.335
The Fingers	0.6035	0.0711	6.409 (4 schools)	5.486	40.47	92.20	2,212.03	0.510
Nelson Island	0.7587	0.3010	3.924 (2 schools)	9.514	27.44	78.59	3,467.75	0.749
3 above areas pooled[1]			3.775	1.151				
Halibut Hill	1.4810	0.2028	9.639 (25 schools)	21.668	28.81	411.27	51,758.47	0.553

[1]School biomass data from Heceta, The Fingers, and Nelson Island were pooled to provide a mean school biomass which was used to calculate total biomass in each area.

TABLE 8.—Summary of estimates of school abundance (D), mean school biomass (MSB), and biomass (B) of widow rockfish on the Halibut Hill ground during replicates on 26-27 March, 30 March, and 31 March-1 April 1982.

Sampling period	No. of replicates	No. of schools sighted/ replicate	$\hat{D}$ (schools/km^2)	$\hat{Var}(\hat{D})$	$\hat{MSB}$ (t/school)	$\hat{Var}(\hat{MSB})$	Area (km^2)	$\hat{B}$ (t)	$\hat{Var}(\hat{B})$	$CV(\hat{B})$ $[\hat{Var}(\hat{B})]^{1/2}/\hat{B}$
26-27 March	3	9 14 13	0.394	0.1264	21.674 (MSB based on 8 schools)	153.878	28.81	245.96	52,852.69	0.935
30 March	1	34	4.499	0.8908	0.729 (MSB based on 7 schools)	0.160	28.81	94.49	2,962.75	0.576
31 March-1 April	3	9 11 11	1.325	0.1687	0.935 (MSB based on 9 schools)	0.088	28.81	35.69	238.52	0.433

Variations in the pattern of school abundance over the course of a night were common. Echograms recorded during the seven replicates of one transect on the Halibut Hill ground (Fig. 11) illustrate one case when abundance was high early in the night and decreased toward dawn (26-27 March). The opposite trend of low abundance increasing toward dawn is illustrated (31 March-1 April) in the same figure.

DISCUSSION

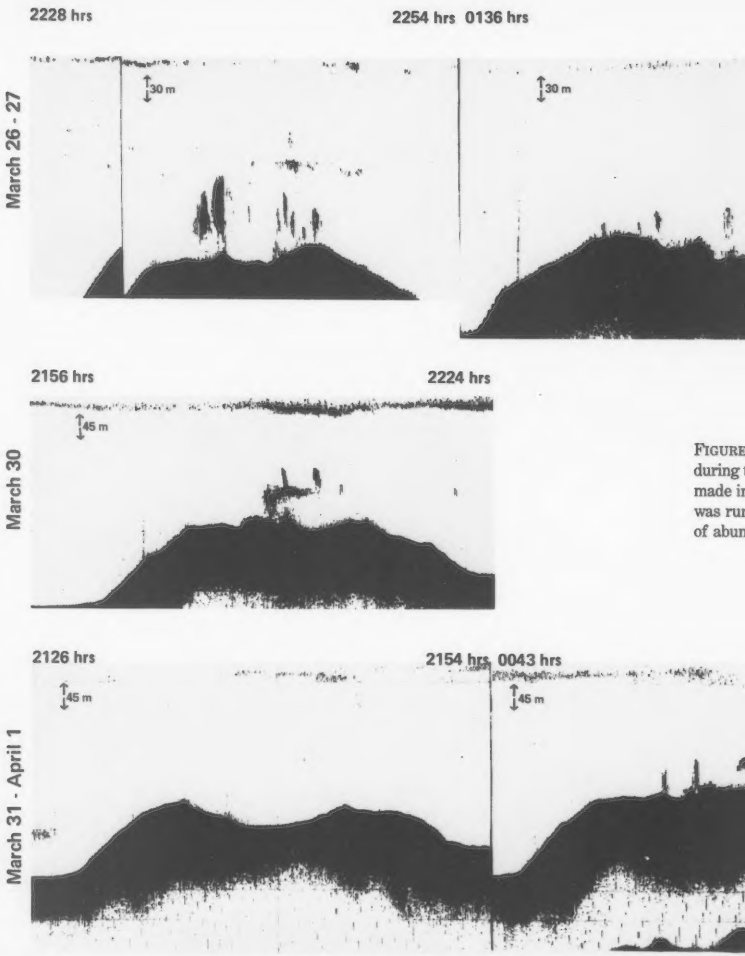
The objectives of this 3-yr project were to study the schooling behavior of widow rockfish to provide the background needed to design effective abundance estimating surveys; then to develop an appropriate survey methodology for the species; and, finally, to test the feasibility of implementing such a survey. Substantial progress was made toward satisfying these objectives. The studies of widow rockfish habits and distribution have provided a base for designing surveys which cover its range and produce the best likelihood of encountering the exploitable population at a time when it will be most available.

Understanding the schooling and dispersal behavior of widow rockfish was important to develop an appropriate survey approach for estimating abundance. The nighttime aggregations which are the targets of the commercial fishery tend to disperse about daybreak, perhaps scattering throughout the water column or seeking shelter near the bottom. If the latter had been the case, more conventional survey methods (i.e., bottom trawl or conventional echo integration surveys) might have been more appropriate.

Although daytime concentrations of widow rockfish were observed, bottom trawl catches during the 1980 and 1981 surveys showed that this species is relatively unavailable to bottom trawls in an area where widow rockfish are known to aggregate at night.[10] This is substantiated by low incidences of widow rockfish in catches of other bottom trawl surveys during periods when midwater trawlers were making large landings. Consequently, when midwater schools disappear during the day, it is unlikely that they disperse along the bottom. In recent years, skippers of midwater trawlers have commented that widow rockfish are becoming more evasive and dive below their nets to avoid capture. Some skippers have taken advantage of this behavior by purposely driving the schools toward bottom with engine noise where they capture them with bottom trawls equipped with roller gear. Although these are classified as bottom trawl landings, the fishermen are, in a sense, capturing midwater schools. Fishermen have also reported encountering daytime aggregations of this species over the continental slope in waters deeper than they are usually found at night (>500 m) and some have been able to catch them on or near the bottom during the day. Thus the distribution of widow rockfish relative to the sea bottom is quite unpredictable during the daytime. These schools are also not as large as those that occur at night. The appropriate time to survey this resource thus appeared to be at night. The line transect survey method, adapted for use with sector scanning sonar and echo integration equipment, was chosen over conventional echo integration and the line intercept method because of its ability to survey areas more quickly and thoroughly.

Application of the method exposed several problems affecting the precision and accuracy of the abundance estimates. The estimation of school abundance was hampered primarily by limitations of the sonar equipment and by small samples. We were not

[10]Observations of midwater echosign and landing information from commercial vessels fishing in the area confirmed that the usual dense midwater widow rockfish aggregations were present in the area at night during the 1981 bottom trawl survey.



FIGURE
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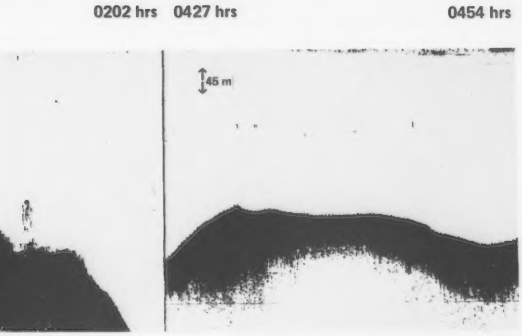
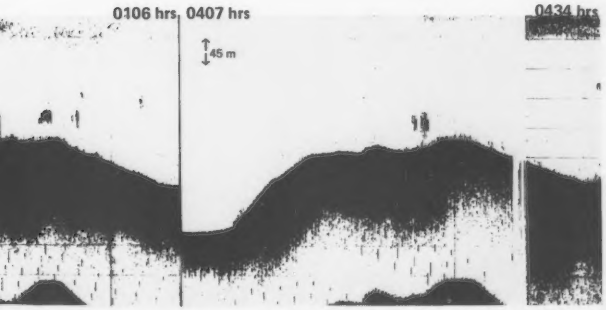


FIGURE 11.—Echograms of Halibut Hill Transect No. 4, which was replicated seven times during the three separate sampling periods. Each row of echograms represents all replicates made in a given night. Columns roughly correspond to the time of night that the transect was run. Sunrise occurred at about 0610. Temporal variability can be seen in the pattern of abundance of widow rockfish schools in the area.



able to calibrate the sonar systems so that the sensitivity of all transducers in the array were equal. Hence, the probability of detecting a given school in one sector of the sonar display was not necessarily the same as detecting it at an equal distance in another sector. The inability to calibrate the transducers may have compromised our ability to detect all schools directly below the transect. This is the most important assumption of line transect surveys; school abundance estimates will be biased downward if it is violated. Intercalibration of the transducers would also help establish a more accurate detection function which would apply throughout the sonar's range.

The limited lateral resolution of sector scanning sonar hampers the accurate measurement of school width, an important value for determining mean school biomass. Each transducer in the fan-shaped array acts as an independent echo sounder and if any portion of a school enters the radiation pattern, the entire width of the 9°-10° sector sampled by that beam will be displayed as a reflective target (Fig. 12). This results in an overestimation of school width and a distortion of the school's size and location, yielding overestimates of biomass and inaccurate measures of distance from the transect plane. The detection function will be altered by these inaccuracies and may modify estimates of school abundance depending on the magnitude and the direction of the errors. The distortion may be aggravated by interference of side lobes in the directivity pattern of individual transducer beams (Fig. 13). Even these lower power lobes can produce echo signals if very dense targets are encountered and may interfere with the acoustic signals from adjacent transducers.

Another weakness of sector scanning sonar in this application is insufficient detection sensitivity. This weakness became apparent during calculations of the lengths of individual schools. Lengths were calculated twice for each school, once based on echo sounder data and again based on sonar data. The theoretically correct method would employ the sonar data because schools could be detected further to each side of the vessel. The echo sounder could only detect the portion of the school within the 10°-11° beam directly below the vessel. Consequently, if a large part of the school was outside the beam, its length was underestimated. In practice, however, the length estimates based on sonar detections were usually shorter than those based on echo sounder data (Table 9) due to the lower sensitivity of the sonar system. The sonar-based lengths were chosen, however, because they measured the dimensions of the part of the school having densities above the threshold required to trigger the sonar. This is probably

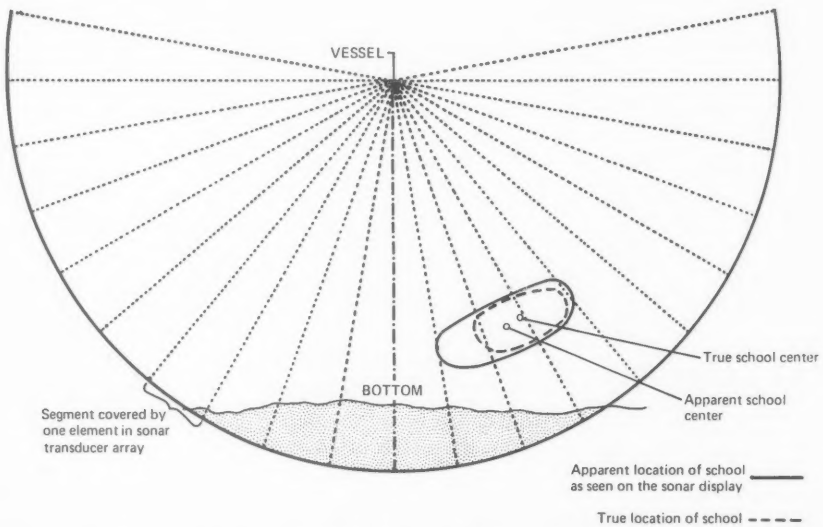

VESSEL
BOTTOM
True school center
Apparent school center
Segment covered by one element in sonar transducer array
Apparent location of school as seen on the sonar display
True location of school

FIGURE 12.—A facsimile of the sector scanning sonar output display exemplifying biases in apparent school locations resulting from the limited resolution of the instrument.

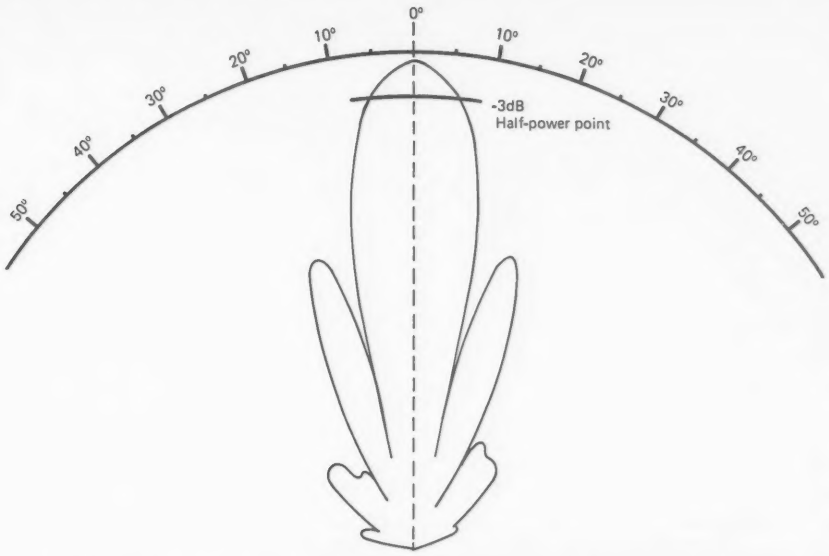


FIGURE 13.—The theoretical directivity pattern of one transducer element of the sector scanning sonar showing side lobes which may interfere with the signals received by adjacent transducers.

a more proportional measurement of school length than the echo sounder-based lengths. The accuracy of school dimension measurements could be improved by using more sensitive and specialized sonar equipment.

These problems with the limitations of sector scanning sonar should not be difficult to overcome. More sensitive quantitative sonar equipment is now available or relatively easy to develop. Lateral resolution may remain a problem because of the difficulty and expense of producing narrow-beam transducers, but the errors it causes are relatively unimportant.

The accuracy of mean school biomass estimates would be improved by target strength studies specific to widow rockfish. Calculation of average fish density within each school was relatively straightforward but involved assuming a target strength of −35 dB/kg. Ideally, the target strength should be calculated specifically for widow rockfish but such specialized work was beyond the scope of this study.

The ability to distinguish widow rockfish schools from those of other species using hydroacoustic equipment is an important element of this technique. Through these studies, our ability to correctly identify widow rockfish echo sign has been improved. The accuracy of species identification varies depending on the nature of the species complex in the survey area. Where shortbelly and redstripe rockfish are present, the potential for misidentification increases. Technological improvements in sonar equipment may help to reduce this problem. The density of a school is an important criterion for distinguishing widow rockfish from other species and newer sonar equipment includes density-graded color video displays. Other techniques, such as underwater photography or remote video camera vehicles, might also improve our ability to identify species. I believe, however, that test fishing will always be a necessary component of hydroacoustic resource assessment surveys.

Surveys of widow rockfish resources must be designed with the behavior and distributional variability of the species in mind. The diel behavior of the species indicates that the most effective sampling period is at night, but even then unpredictable behavior places special demands on survey design. Observations from hydroacoustic transects which were replicated on several nights (Fig. 11) show that long-term variability in abundance (e.g., night-to-night or week-to-week) is even more marked than that over a shorter time. These results are substantiated by other surveys (see footnotes 5, 7, and 8) and illustrate the difficulty of estimating widow rockfish abundance. Long-term variability is also a factor in area-swept bottom trawl surveys. The

TABLE 9.—Comparison of school length measurements (m) derived from echo sounder versus sector-scanning sonar data collected aboard the FV *Ocean Leader*, 14 March-7 April 1982.

School	Density (kg/m^2)	Length from echo sounder	Length from sonar
1	0.1292	48.5	45.0
2	0.0265	85.8	2.1
3	1.4860	66.2	5.8
4	1.6996	51.8	19.2
5	0.6374	37.4	74.0
6	0.3559	37.4	79.6
7	1.2415	59.9	52.3
8	0.7513	93.2	66.5
9	0.2119	117.5	118.1
10	0.7567	81.9	236.2
11	0.0686	526.9	497.5
12	0.0453	45.0	31.9
13	0.0490	96.9	353.1
14	0.0068	138.0	18.7
15	1.1400	511.9	393.2
16	0.6089	189.7	64.2
17	0.3055	76.6	18.4
18	0.4564	84.6	70.6
19	0.2154	27.8	93.0
20	0.0080	62.5	116.6
21	0.0487	103.0	16.9
22	0.1057	130.3	49.3
23	0.0936	147.5	28.5
24	0.1730	27.4	9.9
25	0.0103	46.8	39.6
26	0.1262	53.6	40.9
27	0.0182	67.7	43.9
28	0.1013	30.1	124.9
29	0.0830	67.7	84.2
30	0.0430	67.7	189.4
31	0.0208	48.9	33.5
32	0.0117	23.8	41.4
33	0.0128	22.4	14.8
34	0.1808	106.4	50.2
35	0.1809	292.2	216.7
36	0.0424	81.0	66.4
37	3.3097	158.3	101.6
	$\bar{x}$ 0.3990	105.8	94.8
	s 0.6587	113.5	112.2

assumption is that the variability has a strong random component and catch per unit effort values are consequently unbiased. The same situation may well be true here, in which case an important component of the survey design would be multiple replication to obtain good estimates of both long- and short-term variance.

Burnham et al. (1980) reported that good results from line transect surveys require observation of a minimum of about 40 objects per replicate. Fitting the observed perpendicular sighting distances to a detection function becomes less reliable with a smaller number of objects. Widow rockfish abundance is now low on all major grounds and the recommended minimum number of schools was not observed during any single replicate in the 1982 survey, but by pooling replicates a sufficient database was constructed. Sample sizes could be increased through more intense sampling. A time-stratified analysis of the data would be desirable to define within-night variability, but this would place even further demands on a sampling program.

Surveys of the type used for widow rockfish must cover the geographic range of the species of interest more thoroughly than most other survey methods. The dynamic behavior of widow rockfish suggests that the survey method should cover large areas in a relatively short time in order to survey a given fishing ground at least once during the night. Because of day-to-day variability, surveys should include sampling each area during several nights over a 1- or 2-wk period. Most areas containing fishable widow rockfish concentrations have probably been identified and there are a limited number of these grounds (probably 12-20); nearly all are characterized by ridges or rises on the outer continental shelf or upper slope and are relatively small in area. Intensive sampling of widow rockfish, therefore, is more feasible than for most other groundfish species inhabiting less well-defined areas.

Because widow rockfish schools are continually forming and breaking up, there may be a significant portion of the population which is not schooling at any given time and is therefore not susceptible to these survey techniques. This project did not answer whether this is so, but nothing was found to suggest that widow rockfish are significantly detectable by trawl or hydroacoustic surveys in any form other than midwater schools. Until more is learned about the proportion of the stock occurring as schools, surveys must be considered as yielding minimum biomass estimates. Clark and Mangel (1979) proposed a study of rates of school formation and dispersal to explain and evaluate a similar relationship between overall stock size and the proportion of a yellowfin tuna stock occurring as schools. Such a technique should receive further consideration in this situation, but present low widow rockfish school abundance ($schools/km^2$) and lack of a consistent pattern of school formation and dispersal would probably make its application in widow rockfish assessment difficult. This question is analogous to that of defining catchability coefficients (i.e., what proportion of those fish in the path of a net are actually captured) for quantitative trawl surveys. Changes in relative abundance can be monitored by such surveys without knowing the catchability if one assumes that the available proportion of the population is constant.

Results of other analyses of widow rockfish be-

havior and stock size should be used to evaluate survey methodology. The groundfish management team of the Pacific Fisheries Management Council (see footnotes 2 and 3) used stock reduction and cohort analyses to estimate the abundance of this species. In an area comparable to our 1982 survey area, the widow rockfish biomass was estimated to be 21,664 t at the begining of 1982. This estimate is based in part on commercial landing information and, consequently, the definition of the grounds to which it applies is somewhat vague. The fishery-based estimates are much higher than those derived from the 1982 survey data (about 830 t). The relatively low sensitivity of the sonar systems used would result in underestimating biomass and is undoubtedly responsible for much of this difference. The discrepancy is also partly due to the fact that our survey methods only estimate the portion of the stock present as detectable schools and are therefore a measure of relative, rather then absolute, abundance. This is true to some extent for most types of surveys.

Innovations are also needed to resolve the technical problems related to data collection, identification of school species composition, and survey design. Some suggestions include

1) a two-vessel survey to improve the efficiency of data collection—such a technique would separate the chore of delineating areas of widow rockfish aggregations, estimating school abundance, and test fishing from that of estimating mean school biomass (Gunderson et al. fn. 7);

2) a means of recording a time base on both the audio and video tape records of the echo sounder and sonar to simplify finding the same school on each system for school dimension measurements; and

3) a method of estimating all school dimensions and the density within the school from a single data collection system—this would entail development of a sophisticated, quantitative sonar-integration system with the capability of recording the output onto videotape (Ehrenberg 1979).

Such refinements could probably be implemented with relative ease. The methodology should be re-evaluated when these technological and sampling improvements have been made. Widow rockfish management could have been significantly improved with the knowledge of stock size from an effective resource assessment survey. There are also other species which exhibit similar behavior and which, although presently unexploited, need to be assessed (e.g., shortbelly, redstripe, and black rockfish). This methodology could probably be easily adapted for surveying these resources.

CONCLUSIONS

Based on the results of research conducted during this project, the line transect survey method using a sector scanning sonar and a quantitative echo sounder appears to be the best means of assessing widow rockfish abundance with research surveys. A weakness of this method is that it only measures the portion of the population existent as distinguishable schools and that portion may be quite variable. It also relies heavily on subjective experience for identifying the species composition of schools. Its strengths are that large areas can be covered quickly and it is not necessary that all schools within sighting range be detected in order to estimate school abundance. It appears that this could be a useful assessment method for widow rockfish and for several other Pacific coast groundfish species which are not yet being seriously exploited. The effectiveness of the technique could be enhanced by employing or developing more sensitive and specialized quantitative sonars and by improving the methods of data collection. The technological and survey design problems encountered should be relatively easy, though somewhat costly, to resolve. The method should then be reevaluated to determine its utility. As the technique is used, scientists will gain a better understanding of the behavior and habits of the target species.

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POPULATION AND FISHERY CHARACTERISTICS OF GULF MENHADEN, *BREVOORTIA PATRONUS*

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ABSTRACT

Landing data from 1964 to 1978 for the purse seine fishery in the north-central Gulf of Mexico for gulf menhaden, *Brevoortia patronus*, were analyzed to determine growth rate, yield-per-recruit and spawner-recruit relationships, and maximum sustainable yield (MSY). Estimates of stock size, year-class size, and rates of fishing were obtained from cohort analysis. The fishery is characterized by high rates of both fishing and natural mortality. During the period studied, an average of 40% of the population of age-1 and older fish were taken by the fishery and 47% was lost to other causes annually. Although there was substantial scatter about the fitted curve, a Ricker-type spawner-recruit relationship was found to be suitable. The number of age-1 recruits fluctuated annually between 7.5 and 25.4 billion during the period studied. Maximum biomass of a year class is reached at an age of about 1.5 years. Yield-per-recruit estimates were obtained for an array of fishing mortalities and ages of entry. A deterministic simulation model incorporating growth, the spawner-recruit relationship, and age-specific rates of fishing provided an estimate of MSY at 585,118 t with 127% of the current mean rate of fishing. Implications for the current and future status of this fishery are discussed.

Gulf menhaden, *Brevoortia patronus*, are filter-feeding, surface-schooling clupeids that are subjected to an intensive purse seine fishery in the northern Gulf of Mexico. Although annual landings have fluctuated, there has been a general increase since the inception of the modern fishery in 1946 to a high of 820,000 metric tons (t) in 1978. The fishery consists of about 80 refrigerated vessels serving 11 reduction plants at 6 ports in Mississippi and Louisiana. The fishing season is currently set by State law from mid-April to mid-October. Although a majority of the catch is taken off Louisiana and Mississippi, vessels range west into eastern Texas coastal waters and east to the coastal waters of the Florida panhandle. Vessels, aided by spotter aircraft, land from 6,000 to 10,000 t/6-mo fishing season. Excellent background information and descriptions of the fishery have been published by Christmas and Etzold (1977) and Nicholson (1978).

Considerable literature exists on the general biology of gulf menhaden (Reintjes et al. 1960; Reintjes 1964; Reintjes and Keney 1975; Christmas and Etzold 1977); however, information is scarce on the population dynamics of gulf menhaden and on the dynamics and impact of the fishery. Chapoton (1972) and Schaaf (1975a) estimated maximum sustainable yield (MSY). Ahrenholz (1981) described recruitment patterns and estimated natural and fishing mortality rates from returns of tagged juvenile and adult menhaden.

Gulf menhaden have a life history similar to many other estuarine-dependent coastal species. Spawning takes place in coastal and offshore waters in the winter (Christmas and Waller 1975[3]; Lewis and Roithmayr 1981). Larvae move onshore into Gulf estuaries in winter and early spring, transform to juveniles, and remain in the nursery areas until the following fall. Juveniles move offshore during the winter and back into coastal waters the following summer. Spawning occurs for the first time at the end of their second year.

A joint State-Federal-Industry plan developed for gulf menhaden identified the lack of a reliable measure of effective effort and questionable MSY estimates as major concerns in evaluating the gulf menhaden stock and fishery (Christmas and Etzold 1977). Problems encountered in determining the status of gulf menhaden stocks and estimating a long-term yield from catch-effort data on schooling species subjected to a purse seine fishery are compounded by the "dynamic aggregation process" described by Clark and Mangel (1979). Basically, they

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hypothesized that surface schooling species are more susceptible to fishing effort than nonschooling species, and indicators of abundance such as catch and catch per unit effort (CPUE) are not reliable when the "intrinsic schooling rate is greater than the intrinsic (population) growth rate". Thus, severe stock depletion could occur in the gulf menhaden fishery before indications of such a situation were evident from catch and CPUE data. The dynamic aggregation process may be further aggravated when the vessels are assisted by spotter aircraft which greatly reduce search time.

We have attempted to estimate characteristics of the gulf menhaden stock, such as population size, biomass, growth rate, spawner-recruit relationship, and to determine characteristics of the fishery, such as fishing mortality, catchability coefficient, yield-per-recruit, equilibrium yield levels, and MSY. These characteristics were determined through application of cohort analysis, yield-per-recruit and spawner-recruit models, and a deterministic simulation model of the Gulf of Mexico population and fishery. Our overall objectives are to evaluate the status of the gulf menhaden stock, determine the impact of the fishery, and provide an outlook for the stock and fishery for resource managers and the purse seine fishing industry in the Gulf of Mexico.

GULF MENHADEN DATA BASE

The National Marine Fisheries Service (formerly Bureau of Commercial Fisheries) has maintained a sampling program for gulf menhaden since 1964. Details of the sampling methodology are given by Nicholson (1978) and Huntsman and Chapoton (1973), and a description of the aging technique is provided by Nicholson and Schaaf (1978). Vessel landings by trip have been recorded, along with pertinent data on vessel size and characteristics. Overall summaries of landings by year and nominal effort (measured in vessel-ton-weeks) are available back to 1945, but the basis for the bulk of this analysis is the catch and effort data (1964-79) and estimated number of fish landed at age for these years (Table 1).

WEIGHT-LENGTH RELATIONSHIP AND GROWTH

Estimates of growth rate are needed for yield analyses and estimates of size at age are needed to determine the spawner-recruit relationship. Although some calculations use length and others weight, all growth estimates were calculated for length, and when required, weight was estimated from the weight-length relationship.

For each age group, there was no major systematic variation in the mean length over the 15 yr period (Fig. 1). In addition, no density-dependent correlations were detectable for mean length at age on stock size or on year-class size, estimated from the subsequent cohort analysis. Hence there appeared to be little, if any, potential gain in estimate accuracy by computing and using year-class specific growth rates when reconstructing the historical population biomass and average size at age for the subsequent spawner-recruit analysis, or to incorporate a density-dependent growth function in the subsequent population simulations for total yield.

Estimates of overall mean length at age for each quarter for the year classes that had passed com-

TABLE 1.—Catch, effort, and estimated number of gulf menhaden landed at age for the 1964-79 fishing seasons (1964-78 for number at age).

Year	Catch (metric tons × 10^3)	No. of vessels[1]	Effort (vessel-ton-weeks × 10^3)	Number at age × 10^6					
				0	1	2	3	4	Total
1964	409.4	76	272.9	6.3	3,135.6	1,365.2	108.1	3.9	4,619.1
1965	463.1	82	335.6	46.6	4,888.1	966.3	69.9	1.5	5,972.4
1966	359.1	80	381.3	46.8	3,126.8	850.2	30.5	0.5	4,054.8
1967	317.3	76	404.7	18.7	4,129.2	309.9	10.5	—	4,468.3
1968	373.5	69	382.3	35.4	3,311.5	850.0	27.0	0.2	4,224.1
1969	523.7	72	411.0	10.8	5,766.8	1,011.1	30.4	—	6,819.1
1970	548.1	73	400.0	49.2	3,256.4	2,197.2	34.4	—	5,537.2
1971	728.2	82	472.9	25.3	5,763.3	1,838.1	166.2	3.7	7,796.6
1972	501.7	75	447.5	17.6	3,146.3	1,615.6	68.7	4.4	4,852.6
1973	486.1	65	426.2	57.2	3,012.4	1,082.7	108.2	1.3	4,261.8
1974	578.6	71	485.5	20.0	3,747.3	1,399.0	60.2	—	5,226.5
1975	542.6	78	536.9	96.4	2,512.3	1,453.1	428.2	0.8	4,490.8
1976	561.2	81	575.9	1.8	4,517.7	1,273.1	190.2	—	5,982.8
1977	447.1	80	532.7	1.6	4,800.2	1,209.6	104.3	7.3	6,123.0
1978	820.0	80	574.3	0.0	6,784.7	2,578.8	48.3	3.6	9,415.4
1979	777.9	77	533.9	—	—	—	—	—	—

[1]Includes only vessels that fished 9 or more weeks.

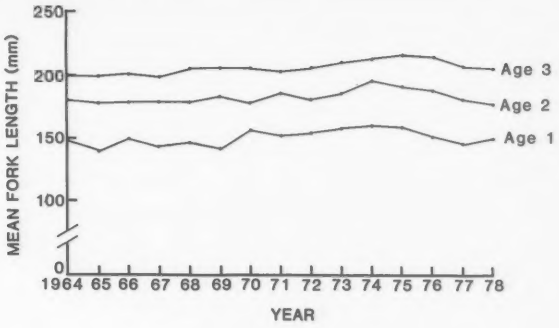

FIGURE 1.—Mean length of gulf menhaden at ages 1-3 taken from commercial landing samples (April-June), 1964-78.

pletely through the fishery were used in the growth computations (Table 2). The von Bertalanffy growth-in length equation

$$l_t = L_\infty(1 - e^{-K(t-t_0)}) \qquad (1)$$

where l_t = fork length (mm) at time t (years),
L_∞ = theoretical length at t = infinity (asymptote),
K = growth coefficient,
t_0 = theoretical age when length = 0

was fitted to the data by the computer program BGC3 (Abramson 1971). Although the data points appear stepped between whole age units, they are reasonably well described by the fitted curve (Fig. 2).

TABLE 2.—Mean length and number of fish sampled at age from 1963 to 1974 year classes of gulf menhaden.

Age	Mean fork length (mm)	Number
1.125	121.7	59
1.375	148.3	43,284
1.625	160.5	57,286
1.875	161.3	1,538
2.125	—	—
2.375	182.9	16,687
2.625	190.6	16,452
2.875	194.4	260
3.125	—	—
3.375	210.5	1,063
3.625	216.4	1,368
3.875	220.2	14
4.125	—	—
4.375	227.8	16
4.625	227.5	32
4.875	—	—

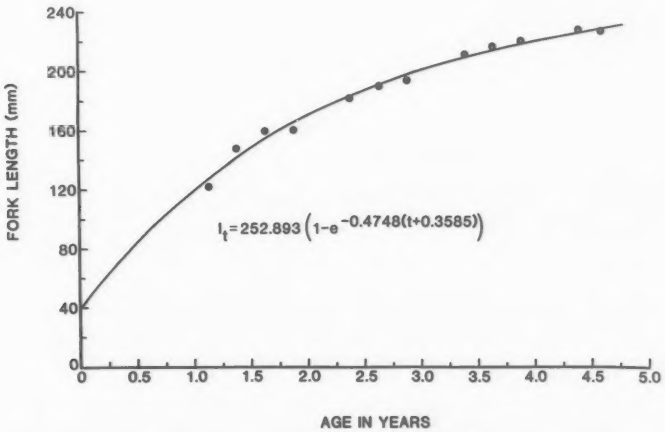

FIGURE 2.—Von Bertalanffy growth curve fitted to average length at age data for gulf menhaden sampled from commercial landings, 1963-74 year classes.

Weight-length regression coefficients were calculated for each of three 2-mo intervals for the major portion of the fishing season for each year class, 1960-77. No systematic variation in the parameter estimates was apparent within years by 2-mo intervals, so the data were pooled between seasons and years. An overall weight-length relationship was obtained from a GM-functional regression (Ricker 1973) on the pooled data. The results are

$$\log_e w = 3.2669 \log_e l - 12.1851 \qquad (2)$$

where w = weight in g, and
l = fork length in mm.

The correlation coefficient (r) was 0.976 and the sample size was 168,397.

COHORT ANALYSIS

Estimates of mortality rates and population sizes were obtained by using the Cohort Analysis technique developed by Murphy (1965) and later modified by Tomlinson (1970). Calculations were made with the computer program MURPHY (Tomlinson 1970). This technique does not involve estimates of CPUE. The backward estimation procedure was used. Since the catch equations and general method of application are given in Tomlinson's paper, discussion here will be limited to the source and nature of input data and parameters.

The calendar year was divided into four periods (quarters) of approximately equal length:

Quarter 1 = 1 January to 3 April,
Quarter 2 = 4 April to 3 July,
Quarter 3 = 4 July to 3 October,
Quarter 4 = 4 October to 31 December.

Numbers of fish at each age landed quarterly were sums of weekly estimates obtained by sampling methods outlined by Nicholson (1978). Annual summaries of these data were given earlier (Table 1).

An estimate of the annual rate of instantaneous natural mortality (M) was obtained from an analysis of mark-recapture data (Ahrenholz 1981). M, equal to 1.1 (0.275 per quarter), was assumed to be constant for all ages and seasons.

Because backward sequential computations, using a range of trial estimates of input F (instantaneous fishing mortality) for the oldest age, tend to converge on the correct value of F for the youngest and forward calculations tend to diverge (unless true starting values are used), it is desirable to begin with the oldest age for which reliable landing data are available (Ricker 1975). Because of aging difficulties (Nicholson and Schaaf 1978), we assumed that catch estimates of older fish, mainly age 4, were not reliable, hence for most year classes estimates of the annual rate of instantaneous fishing mortality (F) for age-2 fish were derived from catches of age 2 and age 3 from

$$F_n = (\log_e C_n - \log_e C_{n+1}) - M \qquad (3)$$

where C = annual catch in numbers at age (n) from a given cohort.

Initial starting values of F for the oldest age group landed in a year class were adjusted by trial and error until the sum of the quarterly F's for age-2 fish were virtually equal to the estimate of annual F_2 derived from Equation (3). This technique was applicable for all year classes except 1960 and 1961, where no 2-yr-old fish were available in the landing data, the 1976 year class where no 3-yr-old fish were available in the landing data, and the 1972 year class, where the 2-yr-old fish apparently were not fully recruited. For the 1960 and 1961 year classes, trial and error adjustments were made to the starting F value until the annual F_3 estimate for the 1961 year class and the annual F_4 estimate of the 1960 year class were virtually equal to the unweighted mean F_3 estimate derived from the sequential computations of the 1963-71 and 1973-75 year classes. Similarly, the mean F_2 estimate was used for the 1976 year class and the mean F_3 estimate for the 1972 year class.

Estimates of number-at-age by quarter by year class obtained from cohort analysis permitted the reconstruction of population structure for the exploited gulf menhaden stock from 1964 to 1977 (Table 3). Numbers of newly recruited age-1 fish varied as much as threefold between years. Because age-1 fish were numerically the most abundant age group each year, the population size fluctuated in close concert with their numbers (Fig. 3).

Resultant age-specific annual F's by fishing season demonstrate that 1-yr-olds are incompletely recruited to the fishery and that age 2's are fully recruited (Table 4). These results are in accord with those of Ahrenholz (1981), who concluded that fish from more distant eastern and western areas of the Gulf of Mexico (Gulf) shifted toward the more heavily fished central Gulf areas as they aged. The slightly higher values for both the weighted and unweighted mean F's for 3- and 4-yr-olds could be due to either small numbers of fish from the most distant eastern

TABLE 3.—Population size (in millions) of gulf menhaden on 4 April estimated by cohort analysis, 1964-77.

Year	Age 1	Age 2	Age 3	Age 4
1964	8,189.2	2,048.0	156.8	5.5
1965	9,796.0	1,329.2	105.0	7.4
1966	5,703.8	1,111.9	41.9	5.2
1967	9,215.6	548.5	14.4	0.0
1968	9,256.7	1,249.0	47.6	0.3
1969	19,311.9	1,539.6	44.6	0.0
1970	12,454.5	3,817.6	59.4	0.0
1971	15,860.1	2,635.0	289.3	4.7
1972	9,580.3	2,704.4	97.0	25.6
1973	15,793.9	1,796.2	181.5	2.6
1974	15,107.1	3,849.3	99.6	0.0
1975	10,220.9	3,324.1	668.4	5.5
1976	11,467.8	2,216.2	435.6	0.0
1977	18,584.2	1,739.4	181.4	57.9

and western areas reaching the more intensively fished waters, or simply a sampling variance. The F estimates from cohort analysis for age-3 and age-4 fish are somewhat suspect, especially for age 4, since the cohort analysis technique used (iterating to a preset F_2) actually makes the F_3 and F_4 estimates of a forward computational nature, rather than backward as for age 1. The divergent nature of the estimates is clearly evident in the values for age 4, although the mean value is realistic for subsequent yield computations, and numbers of fish at this age are of very low magnitude as well.

Because a year class is well represented in the fishery for only 3 yr, a short time span is available for the convergence of estimates of numbers and fishing mortality. This short time span was apparently adequate, however, as cohort runs on the year classes with 4-yr-olds in the landings, using starting estimates of F for age 4 obtained from catch curves, converged to very similar estimates to those obtained by the analysis used here. Ulltang (1977) emphasized that when F is high, convergence is rapid.

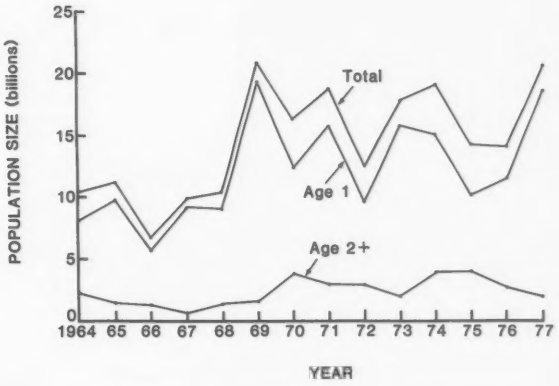

FIGURE 3.—Population number of gulf menhaden as of 4 April 1964-77, Estimated from cohort analysis on 1960-76 year classes.

TABLE 4.—Annual instantaneous fishing mortality rate (F) for gulf menhaden for ages 1-3, by year, 1964-77, and fishing mortality rate applied at age 4 (age 3 for year classes without age-4 landings) to initiate the cohort analysis.

Year	F Age 1	Age 2	Age 3	Age 4
1964	0.7182	1.8706	1.9547	1.9504
1965	1.0757	2.3576	1.9112	0.3546
1966	1.2431	3.2468	2.5992	0.1399
1967	0.8991	1.3447	2.7786	0.0000
1968	0.6938	2.2323	1.4032	[1]10.6065
1969	0.5211	2.1553	1.6225	0.0000
1970	0.4521	1.4760	1.4392	0.0000
1971	0.6681	2.2033	1.3287	[1]10.4097
1972	0.5740	1.6024	2.5195	0.2688
1973	0.3120	1.7933	2.0281	1.2313
1974	0.4140	0.6507	1.7885	0.0000
1975	0.4287	0.9322	1.9484	0.1950
1976	0.7860	1.4030	0.9184	0.0000
1977	0.4375	2.1293	1.4229	0.1923
Mean F (unweighted)	0.6588	1.8141	1.8331	1.8106

[1]Initial F set equal to 10.0.

The short-term impact of the fishery on the stock can be assessed by comparing the estimated number-at-age in the population for any given year with the number-at-age landed by the fishery, or simply by using the estimated rate of fishing and calculating the exploitation rate (u) by

$$u_n = (F_n (1 - e^{-(F_n + M)}))/(F_n + M). \quad (4)$$

From 1964 to 1977 the fishery took an average of 31% of the 1-yr-olds in the population and about 61% of the older fish each year. At these exploitation rates

the population loses 52% of the age-1 fish and 35% of the older fish to natural mortality.

The short-term impact on the entire population was determined by 1) calculating a mean F weighted by the number of individuals taken by age for ages 1-3 and then estimating u by Equation (4) and 2) directly comparing numbers landed with the reconstructed population sizes. The average annual loss of individuals from the population to the fishery was about 40% by both methods. However, recruitment is only partial at age 1, and u is much higher at older ages. Natural mortality losses averaged about 47%/year for the overall population. In the absence of fishing, annual losses to natural mortality would be about 67% for all ages.

A measure of how a unit of fishing effort affects the population is commonly quantified through its effect on F. Traditionally this effect, the catchability coefficient (q), is assumed to be a constant. The total fishing effort times this constant should equal F for the year:

$$F = qf \qquad (5)$$

where f = a unit of fishing effort (here, a vessel-ton-week).

Estimates of q for the 1964-77 fishing years were obtained by solving for q in the above equation for the population F for ages 1-3 ($\bar{F}_{1\text{-}3}$) weighted by number taken at age, and also for the population total F (Table 5). The resultant q's are quite variable (in excess of fourfold). Estimates of q were plotted against corresponding population size to determine if the catchability coefficients were independent of this variable (Fig. 4). An inverse relationship was noted, a situation which also exists for the Atlantic menhaden (Schaaf 1975b). The data were fitted to the power function to demonstrate the curvilinear inverse relationship.

SPAWNER-RECRUIT RELATIONSHIP

The cohort analysis provides estimates of population size at ages 1-4 from 1964 to 1977. All fish mature by the end of their second year, and spawning apparently reaches a peak in December and January (Lewis and Roithmayr 1981). Therefore, estimates of number-at-age in the population as of 1 January were used to provide estimates of spawning stock size and subsequent recruitment (Table 6). Spawning stock was identified as all fish that had reached at least their second birthday by 1 January. Lewis and Roithmayr also showed that length accounted for a greater porportion of the variance in fecundity than either age or weight. Our fecundity estimates, assuming a 1:1 sex ratio, were based on Lewis and Roithmayr's relationship:

$$\log_e E = -9.8719 + 3.8775 (\log_e l) \qquad (6)$$

where E = fecundity in number of eggs and
l = fork length in millimeters.

Because there was little variation in size at age by year class, and the differences noted were not related to population size, estimates of mean length-at-age were obtained from the overall von Bertal-

TABLE 5.—Estimated gulf menhaden population size as of April 4, number caught by year, population exploitation rate (u), estimated population fishing mortality rate (F), population catchability coefficient (q) × 10^{-3}, weighted annual mean fishing mortality rate from cohort analysis ($\bar{F}_{1\text{-}3}$), and the corresponding $\bar{F}_{1\text{-}3}$ catchability coefficient (q) × 10^{-3} calculated from vessel-ton-weeks (Table 1), 1964-77.

Year	Population size (millions) age 1-4	Number caught (millions) age 1-4	Population				
			u	F	$q \times 10^{-3}$	$\bar{F}_{1\text{-}3}$	$q_{1\text{-}3} \times 10^{-3}$
1964	10,399.5	4,612.8	0.444	1.10	4.03	1.0886	3.99
1965	11,237.6	5,925.8	0.527	1.46	4.35	1.2946	3.86
1966	6,862.8	4,008.0	0.584	1.78	4.67	1.6785	4.40
1967	9,778.5	4,449.6	0.455	1.14	2.82	0.9346	2.31
1968	10,553.6	4,188.7	0.397	0.93	2.46	1.0176	2.64
1969	20,896.1	6,808.3	0.326	0.70	1.70	0.7687	1.87
1970	16,331.5	5,488.0	0.336	0.73	1.83	0.8682	2.17
1971	18,789.1	7,771.3	0.414	0.99	2.09	1.0455	2.21
1972	12,407.3	4,835.0	0.390	0.90	2.01	0.9456	2.11
1973	17,774.2	4,204.6	0.237	0.47	1.10	0.7377	1.73
1974	19,056.0	5,206.5	0.273	0.56	1.15	0.4935	1.02
1975	14,218.9	4,394.4	0.309	0.66	1.23	0.7433	1.38
1976	14,119.6	5,981.0	0.424	1.02	1.77	0.9215	1.60
1977	20,562.9	6,121.4	0.298	0.63	1.18	0.7890	1.48

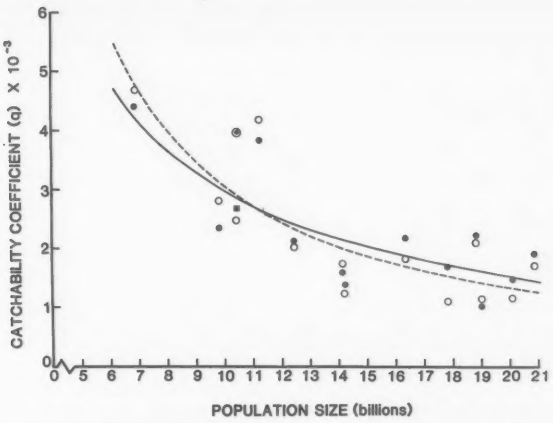

FIGURE 4.—Catchability coefficients calculated from population fishing mortalities (open circles, dashed line), and from cohort annual weighted mean fishing mortalities (dots, solid line) plotted on population number estimated as of 4 April, for the 1964-77 fishing seasons (see Table 5).

TABLE 6.—1 January estimates of number of spawners, number of eggs produced by the spawning stock, biomass of the spawning stock, and number and biomass of recruits at age 1 for gulf menhaden. Preliminary estimates in parentheses.

Year	No. at age (millions)			Total spawners (millions)	No. of eggs (trillions)	Spawning biomass (t)	Resultant recruitment (millions)	Recruitment biomass (t)
	2	3	4					
1964	2,696.3	206.4	7.2	2,909.9	36.1	305,468	12,896.7	410,630
1965	1,749.9	138.2	9.7	1,897.8	23.7	200,150	7,519.5	239,421
1966	1,463.9	55.1	6.8	1,525.8	18.4	156,705	12,138.2	386,480
1967	722.2	19.0	—	741.2	8.8	75,118	12,186.7	388,025
1968	1,644.3	62.6	0.4	1,707.3	20.5	174,454	25,424.7	809,522
1969	2,026.9	58.7	—	2,085.6	24.8	211,752	16,396.8	522,074
1970	5,026.0	78.2	—	5,104.2	60.0	513,461	20,889.9	665,134
1971	3,472.8	382.4	6.2	3,861.4	49.0	412,808	12,618.5	401,773
1972	3,565.3	127.7	33.7	3,726.7	45.2	384,521	20,796.4	662,157
1973	2,365.8	239.0	3.4	2,608.2	32.8	277,323	19,889.0	633,266
1974	5,067.7	131.1	—	5,198.8	61.7	526,725	13,456.1	428,442
1975	4,376.3	879.9	7.3	5,263.5	70.5	588,668	(15,097.7)	(480,711)
1976	2,917.7	573.5	—	3,491.2	46.6	389,073	(24,466.7)	(779,020)
1977	(2,290.0)	238.8	76.2	(2,605.0)	(34.3)	(286,686)		
1978	(5,258.5)	(90.6)	19.2	(5,368.3)	(63.6)	(543,194)		

anffy growth function presented earlier. Thus, length-at-age estimates are taken as constants, and differences in among year estimates of egg production are due to differences in both total numbers and age composition of the spawning stock (Table 6). Similarly, the weight-length relationship was used in conjunction with the mean length-at-age estimates to obtain weight-at-age estimates for computation of spawning and recruitment biomass (Table 6).

Least-square regressions of second and third degree polynomials were run with numbers of recruits on number of spawners to determine the general shape of the spawner-recruit relationship. Dome-shaped functions provided the least residual sum of squares, indicating that a Ricker-type curve (Ricker 1975) is appropriate. A Ricker-type function has been applied to Atlantic menhaden data (Nelson et al. 1977), and the same criteria appear to apply to gulf menhaden data, i.e., that there is a size-dependent fecundity relationship and that adult menhaden are filter feeders which are known to ingest their own eggs. Additionally, the calculation of an index of density dependence, as detailed by Cushing (1971) ($\log_e$ recruitment regressed on $\log_e$ spawning stock), provides a slope of 0.159. This slope,

plus the average fecundity of gulf menhaden (about 25,000 eggs/female) places the gulf menhaden among Cushing's clupeoid groups which have a slightly domed spawner-recruit curve. Accordingly, a spawner-recruite relationship was applied of the form:

$$R = Se^{(S_r - S)/S_M} \quad (7)$$

where R = recruitment at age 1
S = spawning stock size
e = base of natural logarithm
S_r = maximum equilibrium stock
S_M = spawning stock size yielding maximum absolute recruitment.

The model, fitted by a nonlinear least squares technique (Marquardt 1963), predicts an average maximum recruitment of 18.4 billion individuals at a spawning stock of 3.22 billion (Table 7). The curve is a reasonably good fit (Fig. 5), considering the variability inherent in clupeoid recruitment. Data were available over a wide range of spawning stock sizes and recruitment levels. Although recruitment tended to fluctuate widely at lower spawning stock sizes, estimates appear to converge at higher spawning stock levels, indicating the possibility of a strong density-dependent response as spawning stock size increases. The Ricker function appears to describe the data, thus an estimate of spawning stock size premits a general estimate of anticipated recruitment at moderate to high numbers of spawners.

Because fecundity increases with age and because age structure of spawners varies from year to year, estimates of the number of eggs produced should provide a more accurate estimate of spawning stock size than estimates of the numbers of spawners. When the Ricker equation was fitted to number of eggs and number of recruits, the estimate of optimum spawning stock size was similar to the estimate based on the number of spawners and recruits (Table 7) (S_M of 39.66 trillion eggs = 2.3 billion spawners). The unrealistic replacement level (S_r) of 283.32 trillion eggs was generated by scaling factors involved in the comparison of unequal spawner and recruit units (Ricker 1975). Applying the function to spawning and recruitment biomass also provided similar estimates of maximum recruitment and optimum spawning stock size (Table 7,

TABLE 7.—Ricker spawner-recruit estimates of maximum equilibrium stock (S_r), stock size for maximum recruitment (S_m), and recruitment at S_m, for models incorporating number of spawners on number of recruits, number of eggs on number of recruits, and spawning biomass on recruitment biomass, 1964-76 year classes of gulf menhaden.

	Maximum equilibrium stock (S_r)	Stock for maximum recruitment (S_m)	Recruitment at S_m
No. of spawners on no. of recruits	8.83 billion	3.22 billion	18.42 billion
No. of eggs on no. of recruits	283.32 trillion	39.66 trillion	18.48 billion
Spawning biomass on recruit biomass	524,172 t	336,011 t	588,236 t

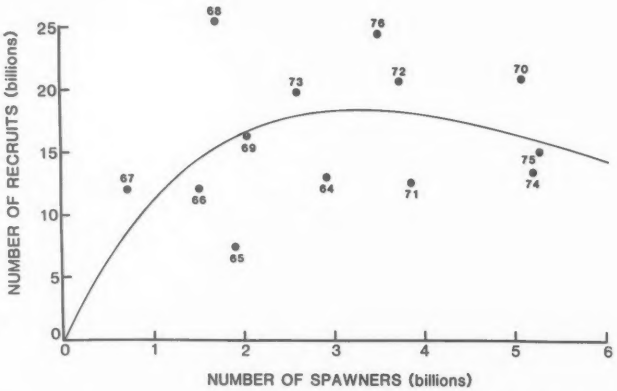

FIGURE 5.—Ricker spawner-recruit relationship for number of spawners and recruits at age 1, estimated as of 1 January, for the 1964-76 gulf menhaden year classes.

Fig. 6). The maximum recruitment level of 588,236 t is equal to about 18.5 billion recruits. The optimum spawning stock biomass of 336,011 t is equal to about 3.2 billion spawners, assuming the age distribution for the spawning stock is average. The function for biomass accounts for changes in age structure of the spawning stock and since age-2 fish consistently represent over 90% of the spawners, differences between plots of numbers and biomass (Figs. 5, 6) are minor.

Spawning stock size has generally remained within a range of potentially good recruitment and has not undergone years of extreme highs or lows (Figs. 5, 6). Trends indicating a steady decrease or increase in stock size and recruitment are not apparent, although the general increased level of recruitment in recent years may be part of a cyclic recruitment fluctuation that is found in many stocks.

YIELD-PER-RECRUIT

We applied what is essentially a Ricker type yield-per-recruit model that was initially developed to evaluate a multiple-gear fishery (M-GEAR) and later modified to accommodate a multiple-area fishery (M-AREA) (Lenarz et al. 1974; Epperly et al. 1979[4]). Yield is summed by time intervals, and individual weights and estimates of natural and fishing mortality can be inserted for each interval (Ricker 1975). An option developed by Epperly et al. (fn. 4) allows for calculation of biomass within intervals by either exponential or arithmetic means. We applied the model in its simplest form: one set of growth data because the stock was not divided into subareas, constant natural mortality rate, and the exponential growth mode for biomass calculation. The year was divided into quarters to simulate the seasonal nature of the fishery (Table 8). Quarterly fishing mortality rates were developed from the cohort analysis. Estimates were obtained for periods of low population size and high fishing mortality (1964-68), high population size and low fishing mortality (1974-77), and "average" population size and mortality (1964-77) (Table 8). Age of entry into the fishery was

[4]Epperly, S. P., W. H. Lenarz, L. T. Massey, and W. R. Nelson. 1979. A generalized computer program for yield per recruit analysis of a migrating population with area specific growth and mortality rates. Unpubl. manuscr., 14 p. Southeast Fisheries Center Beaufort Laboratory, National Marine Fisheries Service, NOAA, Beaufort, NC 28516.

TABLE 8.—Input array of quarterly length (mm), weight (g), and fishing mortality rates (F) used in the calculation of yield-per-recruit of gulf menhaden under average fishing conditions (1964-77), years of low stock size (1964-68), and years of high stock size (1974-77).

Age	Months	$\bar{L}$	$\bar{W}$	$\bar{F}$ (64-77)	$\bar{F}$ (64-68)	$\bar{F}$ (74-77)
0.50	July-Sept.	84.7	10.1	0.0013	0.0018	0.0008
0.75	Oct.-Dec.	103.5	19.5	0.0003	0.0001	0.0005
1.00	Jan.-Mar.	120.2	31.8	0.0002	0.0004	0.0000
1.25	Apr.-June	135.1	46.6	0.1850	0.2677	0.1244
1.50	July-Sept.	148.2	63.2	0.4437	0.6315	0.3593
1.75	Oct.-Dec.	160.0	81.0	0.0299	0.0264	0.0329
2.00	Jan.-Mar.	170.4	99.5	0.0002	0.0000	0.0000
2.25	Apr.-June	179.6	118.2	0.4478	0.5652	0.3683
2.50	July-Sept.	187.8	136.8	1.2213	1.5858	0.8253
2.75	Oct.-Dec.	195.1	154.9	0.1448	0.0594	0.0852
3.00	Jan.-Mar.	201.6	172.3	0.0003	0.0000	0.0000
3.25	Apr.-June	207.3	188.9	0.4500	0.5407	0.2966
3.50	July-Sept.	212.4	204.5	1.2722	1.5752	1.0670
3.75	Oct.-Dec.	216.9	219.1	0.1106	0.0133	0.1557
4.00	Jan.-Mar.	221.0	232.7	0.0000	0.0000	0.0000
4.25	Apr.-June	224.5	245.2	0.1605	0.3085	0.0488
4.50	July-Sept.	227.7	256.7	1.6501	2.3018	0.0480
4.75	Oct.-Dec.	230.5	267.2			

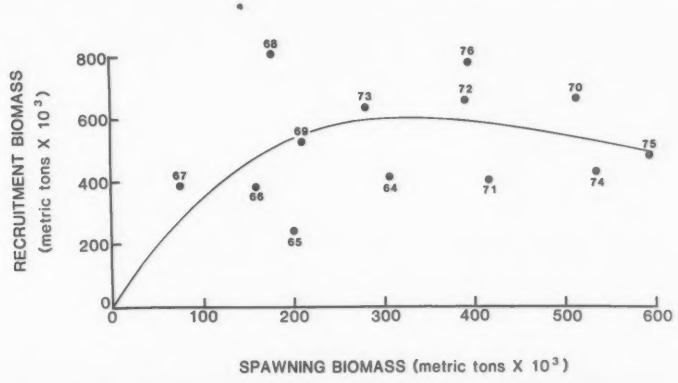

FIGURE 6.—Ricker spawner-recruit relationship for biomass of spawners and recruits at age 1, estimated as of 1 January, for the 1964-76 gulf menhaden year classes.

0.5 yr of age, the age at which gulf menhaden first appear in the catch in extremely small numbers and have a very low fishing mortality rate. Fishing mortality occurs principally during the 2d and 3d quarters of the year (April-September) (Table 8). Various multiples of the average fishing mortality at each age were used to simulate effects of increased or decreased fishing mortality (Table 9).

landings in the fishery of 487,736 t by only 2.6% for 1964-77.

Yield-per-recruit for the years of higher and lower levels of fishing mortality (Table 8) was estimated to be 18.20 and 15.78 g under F-multiples of 1.00 and age of entry at 0.5. Trends were identical to those for average 1964-77 conditions, and thus are not presented in further detail.

TABLE 9.—Estimates of gulf menhaden yield-per-recruit (g) under average conditions of growth and as multiples of average fishing mortality rate (F-multiple = 1.00), 1964-77, at varying age of entry.

Age at entry	Multiplier of fishing mortality									
	0.25	0.33	0.50	0.66	0.75	1.00	1.25	1.50	1.75	2.00
4.50	0.96	1.19	1.60	1.90	2.04	2.34	2.54	2.69	2.79	2.86
4.25	1.06	1.31	1.75	2.07	2.21	2.52	2.73	2.87	2.98	3.05
4.00	1.06	1.31	1.75	2.07	2.21	2.52	2.73	2.87	2.98	3.05
3.75	1.18	1.46	1.96	2.31	2.48	2.84	3.09	3.28	3.43	3.55
3.50	2.73	3.32	4.28	4.93	5.21	5.80	6.20	6.47	6.67	6.81
3.25	3.32	4.01	5.10	5.81	6.12	6.74	7.15	7.43	7.63	7.78
3.00	3.32	4.01	5.10	5.81	6.12	6.74	7.15	7.43	7.63	7.79
2.75	3.63	4.38	5.58	6.38	6.73	7.45	7.96	8.33	8.62	8.86
2.50	6.39	7.62	9.51	10.71	11.23	12.27	12.95	13.41	13.74	13.98
2.25	7.43	8.80	10.86	12.12	12.66	13.71	14.37	14.82	15.14	15.37
2.00	7.43	8.80	10.86	12.12	12.66	13.71	14.37	14.82	15.14	15.37
1.75	7.52	8.91	10.99	12.27	12.82	13.89	14.57	15.04	15.38	15.63
1.50	8.91	10.52	12.93	14.43	15.07	16.36	17.22	17.83	18.30	18.67
1.25	9.45	11.13	13.62	15.15	15.80	17.09	17.94	18.53	18.97	19.30
1.00	9.45	11.13	13.62	15.15	15.80	17.09	17.94	18.53	18.97	19.30
0.75	9.45	11.13	13.62	15.16	15.80	17.09	17.94	18.53	18.97	19.30
0.50	9.45	11.13	13.62	15.15	15.80	17.09	17.93	18.52	18.95	19.28

The yield-per-recruit increases only slightly with a delayed age-of-entry and then drops rapidly because of the high rate of natural mortality. The model predicts maximum cohort biomass at an age of 1.5, before gulf menhaden are fully recruited into the fishery. The high natural mortality rate requires that substantial fishing mortality be applied at a young age if gulf menhaden are to be harvested near their peak biomass.

A three-dimensional representation of yield-per-recruit (Table 9) is helpful in depicting the seasonal nature of the fishery (Fig. 7). Since most of the fishing mortality on age-1, -2, and -3 fish is applied during the 2d and 3d quarters (ages of X.25 and X.50), the impact of delaying recruitment past those quarters results in a sharp decline in yield-per-recruit, due to the high rate of natural mortality.

Predicted catches based on yield-per-recruit were compared with actual catch during 1964-77. Average recruitment at age 1 (16,030 billion), estimated from the cohort analysis, was back calculated to age 0.5, the age of initial entry, and multiplied by the 17.09 g/recruit predicted by the model. The resultant estimate of 474,829 t differs from the average

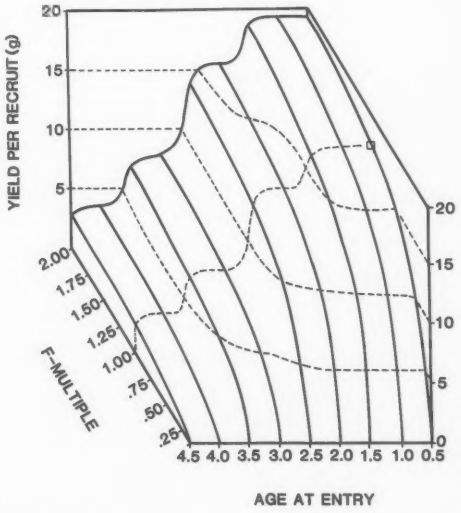

FIGURE 7.—Yield-per-recruit of gulf menhaden under average conditions of growth and with multiples of average fishing mortality by 3-mo interval (F-multiple = 1.0) for the 1964-77 fishing seasons (average conditions indicated by □).

SUSTAINABLE YIELD AND POPULATION SIMULATION

Production functions were developed from the 1946-79 catch and effort data to provide an estimate of maximum sustainable yield (MSY) for gulf menhaden. Application of a standard parabolic surplus production model (Schaefer 1954, 1957) yields an MSY estimate of 553,000 t at 555,000 vessel-ton-weeks. Past updates of MSY for the Gulf fishery have shown continual increases as additional years are added. Chapoton (1972) estimated an MSY of 430,000 t for the 1946-70 period, and Schaaf's (1975a) estimate of 478,000 t included the 1971 and 1972 catch and effort.

For the years in which estimates of catchability coefficient (q) were calculated (1964-77) nominal effort was adjusted to the mean population q of that period. For that time period, mean catchability coefficient was divided by the estimate of population F each year, to provide an estimate of effort adjusted for "average" conditions from 1964 to 1977.

A parabolic surplus production function was applied to the 1946-79 data set, with adjusted effort used instead of nominal effort for 1964-77. The results were similar to model results using nominal effort with an estimated MSY of 541,904 t at an effort of 505,483 vessel-ton-weeks (Fig. 8). A generalized stock production model (PRODFIT) which allows the shape of the curve to vary based on a least squares fit to the data (Fox 1975) was also applied, yielding an estimate of MSY of 636,886 t at an effort of 531,201 vessel-ton-weeks (Fig. 8).

The two curves provide estimates that vary by about 95,000 t with the PRODFIT model indicating a sharp drop in yield after MSY is exceeded.

An estimate of MSY based on biological characteristics should be more reliable than one based on yield and nominal effort, particularly when there is not a clear nominal effort-effective effort relationship. Accordingly, we applied a population simulation model (Walters 1969) for the 1964-77 period which incorporated our estimates of growth, spawner-recruit relationship, fishing mortality, and natural mortality. This estimated the impact of fishing mortality on stock and yield at an array of fishing mortality rates. The model can also iterate to MSY. Underlying assumptions of the Walters' model are that the 1) spawner-recruit relationship incorporated is realistic, 2) array of F's accurately reflect the distribution of fishing effort and availability at age, and 3) time increment estimates of weight are sufficiently brief to realistically estimate both population and catch biomass during the fishing periods. The model calculates population biomass, yield, residual spawners of age 2 and greater, and incoming recruitment. We used weight-at-age data described in the section on average size and growth (Equations (1) and (2)), and used the spawner-recruit relationship developed for the number of spawners and recruits (Equation (7)). The instantaneous natural mortality rate was 1.1 as discussed earlier. Fishing mortality could not precisely mimic that for the fishery, because the program requires either zero fishing mortality or a constant fishing mortality for any within-year increment. However, it does allow for an array of multipliers at a given fishing mortality, providing different F's for each age, if desired. Therefore, we were able to vary fishing mortality by age, but used either zero or a constant fishing mortality for quarterly increments within each year. Since fishing mortality was essentially zero on age-0 fish and was inconsistent between years, a fishing mortality rate of zero was applied to that age group. For age groups 1-4, all of the fishing mortality was by definition imposed equally in quarters 2 and 3 (April-June, July-September), and no fishing mortality was applied in quarters 1 and 4, even though we knew that fishing mortality during the July-September period was consistently higher than that observed for the

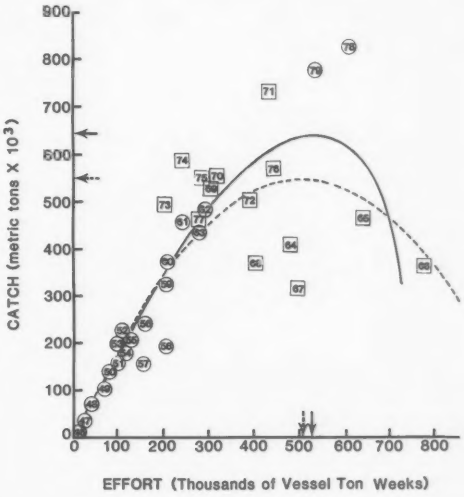

FIGURE 8.—Parabolic (dashed line) and prodfit (solid line) surplus production function models fitted to catch and effort data for the gulf menhaden fishery from 1946 to 1979, with 1964-77 data being estimates of effective effort, based on adjustments from calculated catchability coefficients for those years.

previous quarter (i.e., the same nominal effort was applied to a smaller population). The result was that yield was overestimated for April-June and underestimated for July-September, but estimated reasonably accurately for the season.

We attempted to simulate reality by using multiples of the fishing mortality distribution that we observed in the 1964-77 data base. Fishing mortality imposed to mimic current conditions was obtained by taking the mean fishing mortality at age by quarter from the cohort analysis conducted on the 1960-76 year classes (1964-77 fishing years). The mean mortality on ages 2-4 fish was used, along with a mortality obtained from a scaling factor of 0.362 for age 1 (Table 10). Input population size to start the simulation runs was the mean population number-at-age as of 1 January, the arbitrarily assigned birth date of gulf menhaden. Those numbers were 16,030 million, 2,813 million, 227.9 million, and 10.78 million for ages 1-4. The model was run over a range from 0 to 2.75 times the average fishing mortality and was also used to iterate to MSY under the current distribution of fishing mortality by age (Table 10).

The overall catch-effort curve from multiple runs indicates that the fishery is operating slightly before the MSY level (Fig. 9, Table 10). At the current *F*-multiple of 1.0, the fishery should sustain an average yield of about 565,581 t, assuming no variance in recruitment from the hypothetical spawner-recruit curve.

The model predicts a MSY of about 585,118 t at 127% of the average fishing mortality for the 1964-77 fishing seasons. We feel that this model, which incorporates a spawner-recruit relationship and recruitment pattern plus growth and natural mortality rates, provides a better estimate of long-term MSY than does a model based on a simple catch-effort production function. Considerable fluctuation in yield will result from fluctuations in recruitment, but the long-term MSY estimate appears to be realistic, provided that the estimated spawner-recruit relationship is valid and that the basic pattern of recruitment remains unchanged.

The Walters' model also identifies the level of fishing mortality at which the population is no longer sustainable, i.e., a biological break-even point. The extinction point occurs at an *F*-multiple of 2.50 (150% greater than current fishing mortality), although the model indicates that such extinction would involve a gradual decline over a period of many years, again assuming that "average" conditions prevailed (Fig. 9). Increasing the fishing mortality beyond an *F*-multiple of 2.50 results in a more rapid rate of extinction (Table 10).

Results of low and high *F*-multiple levels show steep slopes on the ascending and descending limbs of the production function curve (Fig. 9). The ascending limb behaves similarly to the curves in the yield-per-recruit model as fishing mortality rates go from low to current levels (Fig. 7). At mortality rates higher than current levels, however, the yield-per-recruit model cannot be used to evaluate potential yield because of the impact of heavy fishing mortality on the spawning stock and the subsequent reduction in recruitment. For example, under the average recruitment level of 16.03 billion fish at age

TABLE 10.—Annual age-specific fishing mortality rates for gulf menhaden, expressed as multiples of the average fishing mortality rate at age, 1964-77, (*F*-multiple = 1.00), actual fishing mortality rates at age used in the population simulation model, sustainable yield, population biomass, and years to stabilization.

F-multiple	Actual *F* at age			Sustainable yield level (t)	Population biomass (t)	Years to stabilization
	0	1	2-4			
0	0	0	0	0	1,268,348	97
0.25	0	0.1647	0.4550	266,878	1,151,345	53
0.50	0	0.3294	0.9100	419,813	1,072,885	35
0.75	0	0.4941	1.3650	512,568	1,009,288	27
1.00	0	0.6588	1.8200	565,581	945,740	8
1.25	0	0.8236	2.2750	585,010	871,695	20
1.27 (MSY)	0	0.8367	2.3114	585,118	865,300	22
1.50	0	0.9883	2.7300	569,823	778,012	32
1.75	0	1.1530	3.1850	514,388	655,278	42
2.00	0	1.3177	3.6400	409,304	492,702	78
2.25	0	1.4824	4.0950	241,462	277,288	210
2.50	0	1.6471	4.5500	0	0	[1]>300
2.75	0	1.8118	5.0050	0	0	[1]250

[1]To extinction.

1 (28.34 billion at age 0.5) and an F-multiple of 2.00, the yield-per-recruit model predicts a total yield of 546,395 t; the population simulation model predicts a gradual decline from current levels and stabilization at about 409,304 t. Thus, when using average recruitment levels and yield-per-recruit results, estimates of yield at F-multiple levels higher than about 1.75 times the average fishing mortality for the 1964-77 period will be unrealistic.

The impact of increasing levels of fishing mortality on the stock is also reflected in estimates of population biomass under an array of F-multiples (Table 10). Biomass estimates were based on predicted population size as of 1 January (i.e., after recruitment and before application of fishing mortality). These estimates show a pre-exploitation population biomass exceeding 1.268 million t, followed by an accelerating decline as increased fishing mortality takes progressively larger fractions of the population and disproportionately larger fractions of older and heavier fish.

STATUS AND OUTLOOK FOR THE GULF MENHADEN FISHERY

The gulf menhaden population appears to be healthy, highly productive, and capable of supporting yearly harvests exceeding 500,000 t, although considerable variation can be expected. It has shown a general increase in abundance through the period covered in this report, although this increase may be a portion of a general cycle of this clupeid stock.

The high natural mortality rate indicates that fishing mortality has to be applied at a fairly high rate and on young fish to avoid loss of surplus biomass. Peak cohort biomass is reached at an age of 1.5 yr. It is not all available to the fishery, because age-1 fish are only partially recruited. Partial recruitment appears to have some benefit in that it affords some protection for the spawning stock.

Recruitment fluctuation appears to be greater at low spawning stock sizes. Initial spawning before full recruitment would assure moderate to high levels of recruitment and reduce chances for large recruitment fluctuation. Therefore, if recruitment failure were to occur, it would likely arise from biotic or environmental factors rather than from excessive fishing mortality.

Significant increases in fishing mortality are unlikely to occur, given the present distribution and operating procedure of the fishery, unless there is a series of recruitment failures. The current fleet of about 80 purse seine vessels appears to be more than adequate to harvest the recruited gulf menhaden stock during years of low to moderate stock size, and

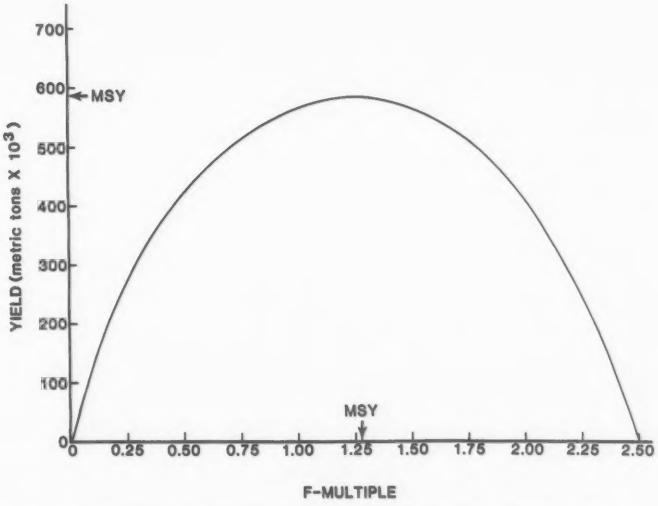

FIGURE 9.—Sustainable yield predicted by a deterministic population simulation model of the gulf menhaden fishery at multiples of the average fishing mortality (F-multiple = 1.00) for the 1964-77 fishing season (see Table 10 for scaling values).

capable of taking advantage of those years when a large harvestable stock is available (1971, 1978, and 1979). Total mortality rates (averaging 83% for age-1 fish and 95% for ages 2-4 fish) are extremely high. Major expansions of the fleet and processing facilities necessary to substantially increase the fishery's share of population biomass would require enormous capital investment. Based on results of the simulation model, large increases in fishing effort would also result in an overall average decline in landings that would likely be followed by an economically forced reduction in effort. Under present circumstances, we do not envision the sustained intensification of effort necessary to drive the gulf menhaden stock to biological extinction.

The simulation model estimates that the effort currently applied in the fishery is probably very close to that which is necessary to produce MSY (Fig. 9), while it exceeds the necessary level in the catch-effort production function (Fig. 8). Assuming that the simulation model reasonably approximates average conditions, some increase in overall yield could be obtained through a modest increase in effort, which has in fact occurred in more recent years.

Based on recruitment levels for 1964-77, it is evident that considerable variation will occur around a long-term sustainable yield level, regardless of the level of fishing mortality. We varied recruitment level in the population simulation model through periods of high (25 billion) and low (10 billion) levels of recruitment to provide estimates of the yield from the fishery under good and poor recruitment regimes, and to observe the rate of response to recruitment changes. The results range from an approximate high of 757,000 t to a low of 303,000 t at the high and low recruitment levels (Fig. 10). Since only age-1 and age-2 fish predominate in the fishery, only 2 years were required for the full impact of a change in recruitment to be shown, with a majority of the impact occurring in the first year. We then allowed the average spawner-recruit relationship to operate, stabilizing yield at 565,580 t. Actual low yield predictions are probably underestimated, in that fishing mortality increases in years of low stock size, and the fishery would produce higher yield than through the fishing mortality imposed under average conditions. Nevertheless, these extremes are near the actual ranges in yield observed in the fishery during the study period (316,100-820,000 t) and should provide reasonable estimates of mean yield and range expected in future years.

Since considerable variation does exist around the spawner-recruit curve and simulations were all conducted in deterministic fashion, the model was run with recruitment varying randomly between the recruitment extremes calculated from our data set (7.5 billion-25.0 billion). The results of that simulation (Fig. 10) provide a long-term (50 yr) average of 467,459 t, but it varies from 718,000 to 263,000 t. We anticipate that the fishery will continue to operate somewhat in this fashion, unless there is a cyclic environmental or biological influence on recruitment.

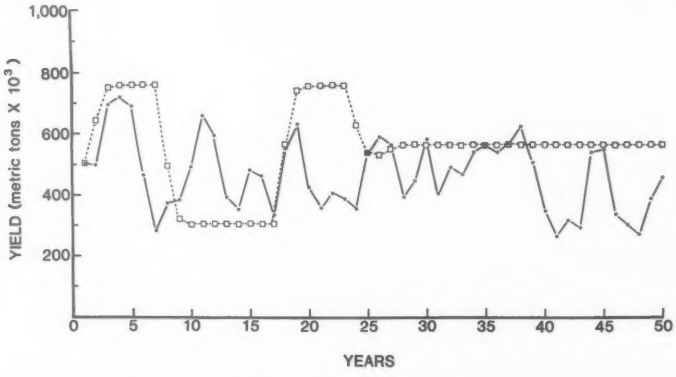

FIGURE 10.—Annual yield of the gulf menhaden fishery projected by the population simulation model when upper and lower values of recruitment from the 1964-77 year classes are inserted (dashed line) and when recruitment varies randomly within limits of observed recruitment for the same data set (solid line).

SUMMARY

The fishery for gulf menhaden appears to be at parity with the stock. There is ample capacity to harvest available biomass and segments of the stock are not available to the fishery until after spawning has occurred. The fishery appears to be near the level of estimated maximum sustainable yield, but will be subject to wide ranges in annual yield. Substantially increased effort will likely reduce long-term average yield, but should not drive the stock to biological extinction. Maintenance of current catch and stock conditions is dependent on the biology of gulf menhaden, the pattern of recruitment, and on maintaining the current fishing strategy. Major changes in the operation of the fishery, such as an expansion of effort east and west of the present range, or offshore on winter spawning concentrations, will change the basis on which these analyses were formulated, and would have consequences which are not predictable at this time.

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LENGTH-WEIGHT RELATIONSHIPS OF BLUE, *PARALITHODES PLATYPUS*, AND GOLDEN, *LITHODES AEQUISPINA*, KING CRABS PARASITIZED BY THE RHIZOCEPHALAN, *BRIAROSACCUS CALLOSUS* BOSCHMA

CLAYTON R. HAWKES, THEODORE R. MEYERS, AND THOMAS C. SHIRLEY[1]

ABSTRACT

Length-weight relationships and condition factors of nonparasitized blue king crabs, *Paralithodes platypus*, and golden king crabs, *Lithodes aequispina*, in southeastern Alaska were compared with crabs parasitized by the rhizocephalan, *Briarosaccus callosus*. Species, sex, and shell condition were considered in all analyses. Parasitized male blue king crabs and parasitized male golden king crabs weighed significantly less than nonparasitized individuals. Golden king crabs may be more resistant to infection and the effects of *B. callosus* parasitism than blue king crabs. They had a lower prevalence of infection, and the percent difference between the body mass of parasitized and nonparasitized crabs was considerably less. In both crab hosts the prevalence of infection was greater in samples where sublegal or smaller size classes of adults were included in analyses, suggesting that crab growth was reduced by the parasite.

A parasite of lithodid crab species in Alaska is the rhizocephalan barnacle, *Briarosaccus callosus* Boschma (Boschma and Haynes 1969; Boschma 1970; McMullen and Yoshihara 1970; Somerton 1981; Hawkes et al. 1985). The parasite's distribution in Alaskan waters, its life history, and its effects on king crab hosts are almost unknown except that parasitized crabs become castrated (Boschma and Haynes 1969; McMullen and Yoshihara 1970). The prevalence of this barnacle parasite varies between areas and species and is especially high in southeastern Alaska. Parasitism by *B. callosus* might decrease the productivity of king crab stocks through sterilization and may also reduce crab growth rates. Therefore, parasitized crabs of the same size as nonparasitized crabs may weigh less. In this study we examined the influence of *B. callosus* on the length-weight relationships and condition factors of parasitized and nonparasitized blue king crab, *Paralithodes platypus*, and golden king crab, *Lithodes aequispina*.

MATERIALS AND METHODS

Two methods were used to compare the growth of parasitized and nonparasitized crabs. A Fulton's condition factor ($w/l^3 \times 10^{-4}$, where w = weight in grams and l = carapace length in mm) was used for comparing different individuals of the same species (Ricker 1975). This method assumes that all body parts grow isometrically. The second method used for comparison assumes allometric growth, where different body parts grow at different rates. Constants were determined empirically by linear regression using the model, $w = AL^B$, and logarithms of the carapace lengths and body weights (Everhart et al. 1976, p. 70-71). The length-weight relationships of parasitized and nonparasitized crabs were compared with analysis of covariance (ANCOVA). All mean values ($\bar{X}$) are given ± 1 standard deviation. Probabilities <0.05 are considered significant and those <0.01 are considered highly significant.

The analysis of length-weight relationships was based on wet weights taken in the field (nearest 25 g) and in the laboratory (nearest gram). Crabs with missing or partially regenerated appendages were not weighed. Carapace lengths were measured to the nearest 1 mm (Wallace et al. 1949). Shell condition was classified according to a four point scale (Somerton and MacIntosh 1983). A new shell condition is found in crabs that have recently molted, and skipmolt crabs are those that have not molted within the last year. Skipmolts or old shell crabs were identified by worn spines and dactyl tips and accumulations of shell epifauna. Infections were diagnosed grossly by the presence of externae or scars, indicative of lost externae. A scar is a short chitinous brown pedicel from which an externa was attached and protrudes from underneath the abdomen.

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Blue King Crab

Male and female blue king crab of various sizes from Muir and Adams Inlets in Glacier Bay (Fig. 1) were measured, weighed, and examined for *B. callosus* by the authors in March 1984. Commercial gear was used but with modified escape ports to prevent loss of juvenile crabs. Data on large male blue king crabs from Lynn Canal and Glacier Bay were also gathered at dockside areas before sale to processors or the public. Since state regulations for southeastern Alaska restrict the commercial harvest of blue king crabs to males ≥165 mm in carapace width, all commercial samples, therefore, excluded females and smaller adult males.

Golden King Crabs

Male and female golden king crabs of various sizes were collected by the authors from Lynn Canal near Haines, AK (Fig. 1), using standard pot gear in May 1984. Commercial catches in November 1983 provided legal sized (≥178 mm carapace width) males.

RESULTS

The prevalences of *B. callosus* in the commercial catches of male blue king crabs were 6.3% and 11.6% for Lynn Canal and Glacier Bay, respectively. Samples from Glacier Bay, which contained males and females of all sizes, had a prevalence of 76%. The prevalence in varisized male and female *L. aequispina* collected from the Haines area was 20%.

Linear length-weight relationships of log transformed data best defined our data, since no trends were present in the residuals (differences between predicted lines and actual data) of parasitized or nonparasitized crabs.

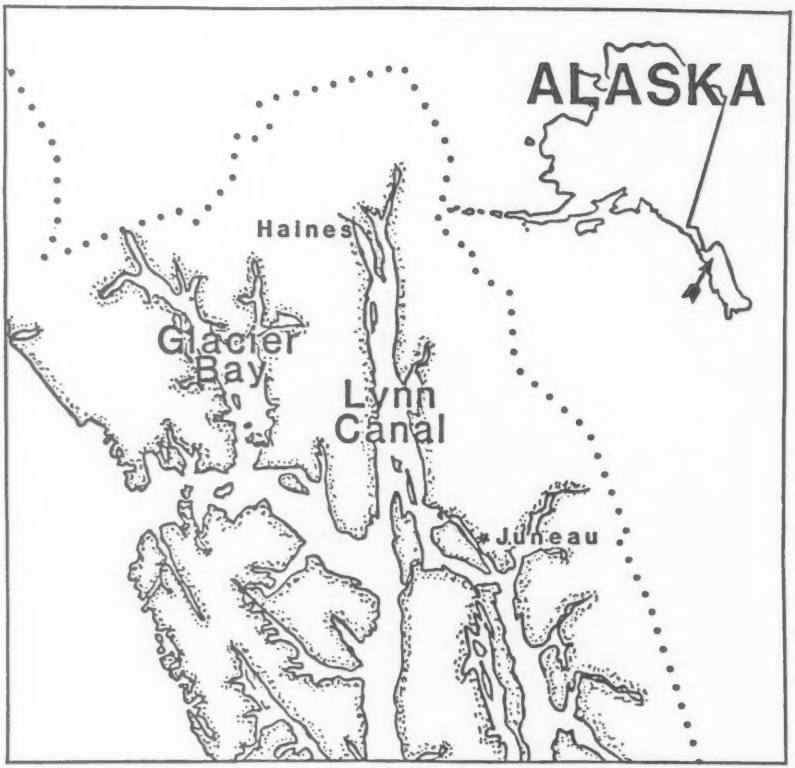

FIGURE 1.—Sampling sites of blue, *Paralithodes platypus*, and golden, *Lithodes aequispina*, king crabs in southeastern Alaska.

Blue King Crab

Glacier Bay and Lynn Canal blue king crab data were pooled. The populations were considered to be identical because the two groups were regarded as having the same linear relationship (ANCOVA). Smaller crabs (<134 mm in carapace length) not common to data sets from both areas and skipmolts were eliminated from this analysis.

Significantly (chi-square test) more skipmolts were found among the nonparasitized crabs (45/237) than the parasitized crabs (9/131). Because skipmolts tend to be heavier than new shell crabs (Somerton and MacIntosh 1983), skipmolting was analyzed as a possible source of bias. In male blue king crabs the new shell crabs had a higher mean weight than the skipmolts at greater carapace lengths, while the skipmolts had a higher mean weight at the smaller lengths (Fig. 2). Although individual linear relationships did not describe the data as well as a common line, the skipmolts were eliminated from further analyses of both blue and golden king crab data.

Subsequently, in the length-weight relationships of male blue king crabs pooled from both areas, with small crabs represented in each group, the nonparasitized crabs were heavier at a highly significant level than the parasitized crabs (ANCOVA) (Fig. 3). Nonparasitized males were 8.7% heavier than parasitized crabs. Nonparasitized male blue king crabs also had a significantly (t-test) higher condition factor (8.5 ± 0.8) than parasitized crabs (7.2 ± 0.6), indicating that nonparasitized crabs were heavier for a given length. Condition factor did not vary with size in nonparasitized blue king crabs but the slope was significant and negative for the parasitized crabs. This indicates that the condition factor of parasitized blue king crabs decreased with increased size.

Only five nonparasitized female blue king crabs were available for length-weight relationships and condition factor comparisons. More samples are needed for further analysis of female blue king crabs.

Golden King Crabs

Males with carapace lengths common to both parasitized and nonparasitized crabs, 117 to 159 mm, provided linear relationships that were parallel and significantly different (Fig. 4). *Briarosaccus callosus* was not present in any of the large commercial-size crabs sampled in 1983; therefore, these samples were excluded from analysis. The percent weight difference between parasitized and nonparasitized male golden king crabs was about 2.6%. Weight conversion in parasitized male *P. platypus* of similar sizes

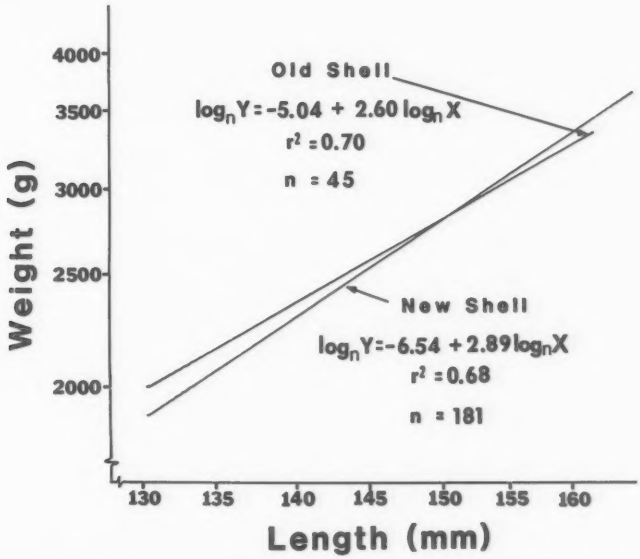

FIGURE 2.—Length-weight linear relationships of new shell and skipmolt nonparasitized male *Paralithodes platypus*.

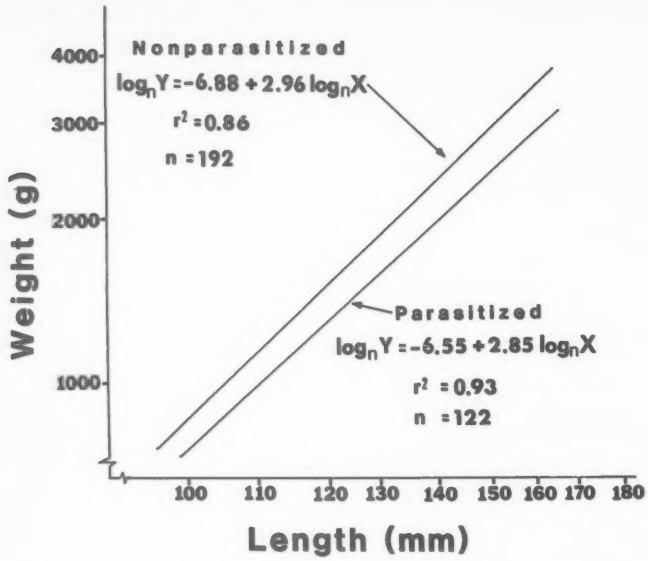

FIGURE 3.—Length-weight linear relationships of parasitized and nonparasitized male *Paralithodes platypus* with skipmolts eliminated.

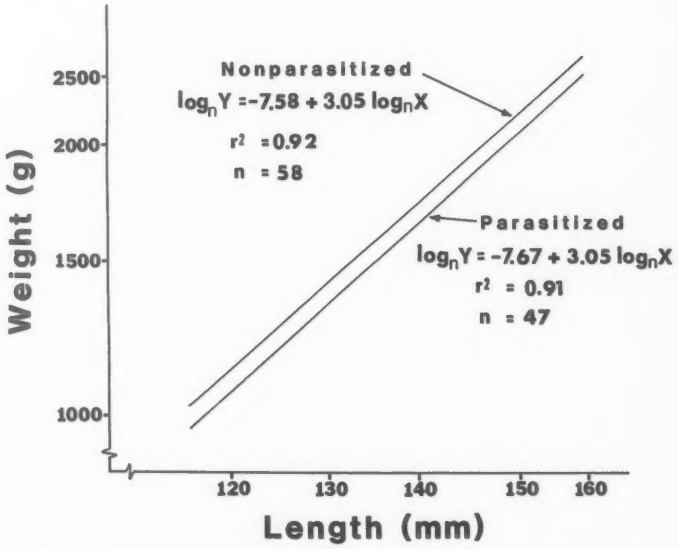

FIGURE 4.—Length-weight linear relationships of parasitized and nonparasitized male *Lithodes aequispina* after elimination of 1983 data.

was inhibited considerably more than in parasitized male *L. aequispina*. The condition factor for nonparasitized male *L. aequispina* (6.5 ± 0.5) was also greater at a highly significant level than for male parasitized crabs (6.1 ± 0.4). The condition factor in parasitized and nonparasitized male golden king crabs did not vary significantly with size.

Nonparasitized female *L. aequispina* (n = 77) were heavier than parasitized females (n = 43) over most of the length range. The linear relationships were significantly different but not parallel, preventing a comparison of the intercepts. Condition factors were not significantly different between the parasitized (5.9 ± 0.5) and nonparasitized (5.7 ± 0.4) females. Condition factors varied significantly with size and in the nonparasitized crabs but not in the parasitized crabs.

DISCUSSION

Weights and, consequently, condition factors were significantly lower in male blue and golden king crabs parasitized by *B. callosus*. A difference in mean weight was also present in female blue king crabs that were parasitized, although an adequate comparable sample size of nonparasitized females was not available. The prevalence of the parasite was considerably greater in king crab populations where sublegal or smaller size classes of adult crabs were included in the sample number. In blue king crabs from Glacier Bay, the inclusion of females in the sample also raised prevalence figures since females had a significantly higher prevalence of barnacle parasitism than male crabs. A potential reason for increased barnacle prevalence in smaller crabs could include differential mortality such that fewer parasitized crabs survive to larger size classes. Other explanations include reduced molting frequencies, reduced number of instars and/or reduced growth represented by a reduction in relative molt increment (Hawkes et al. in press). However, reduced weights in parasitized crabs within the same size classes as nonparasitized individuals suggest that growth of the host crab is decreased by *B. callosus*. The higher parasite prevalence in smaller crabs also supports this conclusion.

Parasitized crabs may develop significantly less body tissue after molting, which is likely to be a cumulative effect occurring over more than one season. Although the complete life history of *B. callosus* is unknown, other species of Rhizocephala are known to require at least 9 to 12 mo to reach reproductive maturity and develop an externa in host crabs (Ritchie and Høeg 1981). In males that become castrated and weight loss of testes is insignificant in total body mass (0.2%) and does not account for the weight difference observed. Also testes weigh less than the interna and externa of the parasite. In female king crabs a considerable amount of the wet body weight can be attributed to the egg clutch and ovaries. Consequently, gonadal atrophy, nonovigerous conditions and reduced somatic growth rates all may account for the lesser weights observed in parasitized female king crabs.

The percentages of weight difference between parasitized and nonparasitized males was considerably different between the two species of king crabs. Golden king crab was less affected by the parasite, sustaining less growth inhibition due to barnacle parasitism than parasitized blue king crabs. Parasitized golden king crabs have significantly higher hemolymph protein concentrations in comparison to either their nonparasitized conspecifics or parasitized blue king crabs. The additional protein may be attributed to the presence of lectins, specific carbohydrate-binding proteins suspected of playing a role in crustacean immunity (Shirley et al. 1985).

If we are correct, reduced crab growth as an effect of *B. callosus* parasitism would conflict with data from other peltogastrid rhizocephalans (O'Brien and Van Wyk 1985). Other rhizocephalan species tend to be more prevalent on larger crab hosts, making enhanced growth or enhanced survivorship a plausible effect of parasitism. Another explanation is that parasitized crabs have less somatic growth and, as a result, have fewer molts. Molting is a time of greatest mortality for most decapods, and those with lower molting frequencies would have greater survival. The probability of infection may also be greater in certain size classes. Behavioral differences or sampling bias could affect the parasite's relative frequency within the host population. Sacculinidae appear to be distributed differently within host populations (O'Brien and Van Wyk 1985). *Pugettia producta* is a majid crab from California and does not molt after reaching maturity. When parasitized by the rhizocephalan *Heterosaccus californicus*, there is no significant effect on molt increments of juveniles and the pubertal molt increment is not affected in adults. However, *P. producta* that are parasitized pass through fewer instars before reaching maturity, and the mean size of these individuals is significantly less than in nonparasitized crabs (O'Brien 1984). Blue crabs, *Callinectes sapidus*, also have retarded growth when parasitized by *Loxothylacus texanus*, with most adults appearing as miniature adult females (Overstreet 1978).

Prevalence of the parasite as a function of host size and field length-weight comparisons are still only indirect measurements of host growth. Consequently, further laboratory studies measuring growth directly in parasitized king crabs are needed to positively prove our hypothesis.

ACKNOWLEDGMENTS

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DISTRIBUTION AND ABUNDANCE OF COMMON DOLPHIN, *DELPHINUS DELPHIS*, IN THE SOUTHERN CALIFORNIA BIGHT: A QUANTITATIVE ASSESSMENT BASED UPON AERIAL TRANSECT DATA

THOMAS P. DOHL, MICHAEL L. BONNELL, AND R. GLENN FORD[1]

ABSTRACT

On 35 aerial transect surveys of the Southern California Bight, 157 sightings of common dolphin, *Delphinus delphis*, schools were observed and mapped for distributional analysis. Sightings were pooled into 30′ of latitude by 30′ of longitude sampling quadrats, and density estimates were obtained by fitting a Fourier series to a frequency distribution of perpendicular sighting distances. Two distinct seasonal distributions are represented by density contour maps: a winter-spring distribution when schools were confined to the easternmost and warmest waters of the area, and a summer-autumn distribution when schools were widespread. Mean seasonal population estimates were 15,448 for winter-spring and 57,270 for summer-autumn (cv of 0.36 and 0.17, respectively). During the warmer water months, the common dolphin population expands its use of the Southern California Bight. They enter from the south, apparently following the major undersea ridges and escarpments, and flow through the Southern California Bight in a generalized counterclockwise fashion. Observational evidence suggests that there is mixing of both the nearshore and pelagic forms of this species in the offshore waters over the Santa Rosa-Cortés Ridge and Patton Escarpment.

The common dolphin, *Delphinus delphis*, is the most abundant cetacean in the waters of the Southern California Bight (SCB). On an annual basis the numbers of common dolphins exceed, on average, the combined total of all other cetaceans in this area by 2.75 times (Dohl et al. 1980).

Common dolphins inhabit subtropical waters of Mexico and the SCB throughout the year (Norris and Prescott 1961). Density estimates for this species and other dolphins (*Stenella* sp.) in waters offshore of Mexico and Central America were calculated by the National Marine Fisheries Service in 1974 (Smith 1981). The distribution of common dolphins in the eastern parts of the Southern California Bight was described by Evans (1975).

In order to understand the role of the common dolphin in the ecology of the SCB and to understand when and where this population is mostly vulnerable to human activities, we have constructed a spatial-seasonal distributional model with two aims: 1) to generate population estimates for the entire area and 2) to describe the general features of seasonal distribution patterns. This is the first study to examine the spatial heterogeneity of common dolphin distribution in the SCB and to generate confidence limits for density and seasonal mean population size estimates.

From April 1975 through March 1978, nearly 110,000 nmi (200,000 km) of combined aerial and ship surveys were conducted within the SCB for the Department of the Interior, Bureau of Land Management (now the Minerals Management Service). During this marine mammal and seabird study, a total of 505 schools of 134,675 *Delphinus delphis* were recorded.

This paper is primarily concerned with one subset of the 3 yr, common dolphin sighting data base. To avoid the statistical pitfalls of pooling data obtained from a variety of platforms performing their missions at different speeds, at different altitudes, and over varying portions of the study area, we restricted these analyses to 35 monthly flights flown at 1,000 ft above sea level (ASL). Each of these surveys required about 15 overwater flight hours and covered about 1,350 nmi (2,500 km) of trackline. All species of cetaceans encountered were recorded as to location, number, behavior, direction of movement, and number of juveniles. Common dolphins were encountered 157 times in this flight series, for a total of 46,153 animals or 69% of all cetaceans observed.

The results of the distributional study and accompanying figures were derived from the 1,000 ft ASL aerial survey data defined above. However, material in the Discussion section draws upon observations made from all survey platforms used during this study.

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METHODS

Aerial surveys were flown at an altitude of 1,000 ft ASL (328 m) at about 90 kn (167 km/h) in a high-wing, twin-engine Cessna[2] 337. The crew consisted of a pilot and three experienced marine mammal observers, one acting as recorder. Surveys were flown along 15 parallel, predetermined tracklines, separated by 15 nmi and extending from the shore to a maximum distance of 100 nmi (185 km; Fig. 1). Tracklines were oriented from northeast to southwest and were roughly perpendicular to the shoreline, as well as to most major features of submarine topography in the study area. Whenever possible, all transect lines were surveyed on each 3-d flight. Transect lines were not replicated on a single survey, nor were they flown in a predetermined order or direction. The first line flown on a given day was occasionally dictated by weather or military activity in the area; subsequent lines were chosen to optimize coverage and simplify logistics.

Observers searched unbounded corridors on each side of the aircraft trackline. Sightings were recorded and coded for computer entry at the time of occurrence. The aircraft was diverted to circle those schools located off the trackline for positive identification, animal count, and photographs. The total animal count recorded for each school was a consensus of the observers on board, derived from multiple orbits of the school. Any additional sightings obtained while "off transect" were not included in later density calculations due to the possibility that the secondary sighting was prompted by the first. All transect segments where observer effectiveness might have been hampered by fog and/or sea state were deleted from the data base; only transect segments where visibility exceeded 1 nmi and the sea state was Beaufort 3 (few, scattered whitecaps) or less were retained.

Aerial photographs were used to validate observer estimates of school size. The aerial photographs were taken on 9″ × 9″ film from a vertically mounted camera and on 4″ × 5″ and 35 mm films in handheld cameras for oblique views. The large, 9″ × 9″ vertical photographs soon proved to be the most useful and were used almost exclusively for count verification. Observer counts and film counts on average-sized schools (up to 100 animals) varied only slightly, but not in a consistent manner. The 3-5%

[2]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

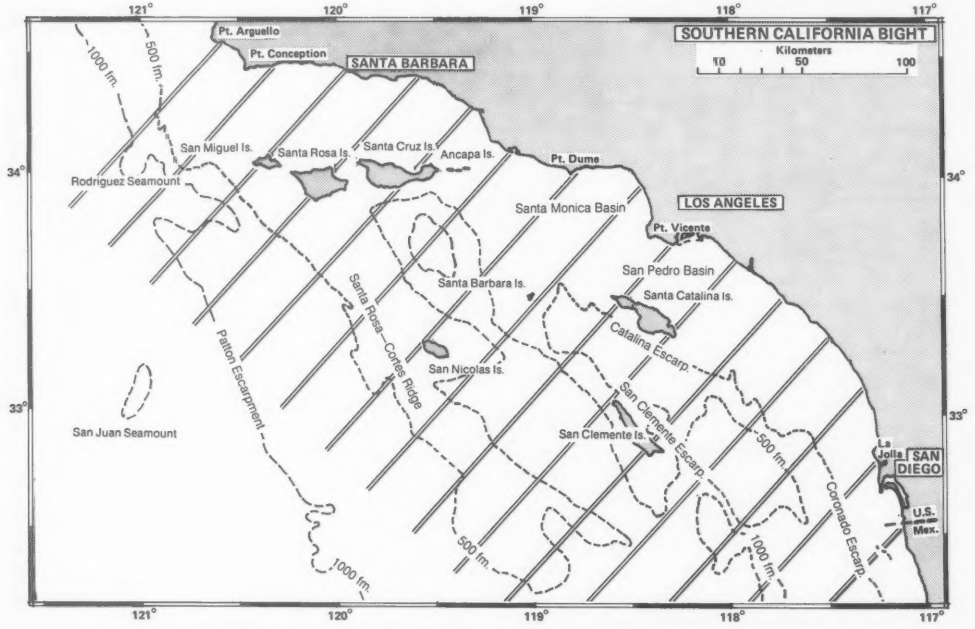

FIGURE 1.—Map of the Southern California Bight study area showing aerial survey tracklines.

variations in counts occurred randomly, with no pattern to indicate in which method the higher counts would occur. Small schools of <100 animals represented most of the sightings (53%). In medium-sized schools, up to 300 animals, the variation was higher (about 11%), and the photographs indicated probable observer underestimation in 62% of the counts. The largest underestimates occurred in large schools, >300 animals, and were found in 76% of the observer counts. These underestimates ranged up to 30% in some circumstances. Within the large-school category, two subcategories became evident: 1) Dispersed schools with multiple discrete subgroups of animals gave the observers less of a problem than 2) the tightly grouped, rapidly moving, compact schools. The dispersed large schools yielded underestimate values in the range of 14-16%, while the compact, large groups were usually 21-23%. Extremely large schools of over 1,000 animals were responsible for the highest error values of up to 30%; these schools accounted for only 6.6% of total sightings.

Generally, we found that aerial estimates were lower than numbers based on photographs and that the larger the school, the higher the difference. We attribute some of the difference to the time lag between when the count was made while circling the school and the photo run over the center of the school. Results of photo runs made either before or after the counting effort did not vary significantly, but occasionally, continued circling scattered larger schools into several smaller subgroups.

Sea surface glare affected observation efficiency to some degree on about 10% of all survey days. Due to the orientation of transect lines, glare conditions could impair the search ability of only the left-side observer on southwest-bound legs (up to 26% of total search effort per survey day). Holt (1984[3]) found density estimates of dolphin schools to be 39% lower under poor sun conditions than during good sun conditions. Using his figure, we calculate that our overall seasonal density estimates might be low by about 1%. Because of the lack of any systematic bias resulting from glare affecting density estimates in one particular region or season more than another, we made no corrections to adjust for this slight underestimate.

The perpendicular distance from the trackline to the sighting was calculated from the declination angle obtained using a hand-held inclinometer. Perpendicular distances were recorded for 112 sightings of common dolphin schools, representing 74.2% of all sightings used in density calculations.

Distributional Model

Inspection of the first year's common dolphin sighting numbers and plots of monthly distribution indicated seasonal fluctuations of residency within the Southern California Bight.

Examination of the 3-yr database showed two distinct seasons of occupancy for the species in the SCB (Fig. 2). A comparison of the two sets of data on a monthly basis show a significant statistical difference ($F_{(1,34)} = 7.66$, $P < 0.01$). In view of these observations, two seasons were defined for the development of the distributional model: a summer-autumn season (July through December) when common dolphin sightings were widespread in the SCB, and a winter-spring season (January through June) when most schools were confined to the southeastern portion of the surveyed area. Common dolphin sightings were assigned by their latitude and longitude to 30′ × 30′ grid-cells (sampling quadrats) centered on degree and half-degree lines of latitude and longitude. Data were pooled to provide seasonal estimates of common dolphin abundance for each 30′ × 30′ grid-cell. The estimate of density of groups in cell i, D_i, was calculated from the relationship:

$$\hat{D}_i = n_i \hat{f}(0)/2L_i \text{ (Burnham et al. 1980)} \qquad (1)$$

where n_i is the number of groups encountered, $\hat{f}(0)$ is the probability density function of perpendicular distances evaluated at the y-intercept, and L_i is the sum of all transect lengths in cell i contributing to the seasonal estimate. The value of the $\hat{f}(0)$ term was calculated using the nonparametric Fourier-series estimator of Crain et al. 1978 (see Burnham et al. 1980 for a complete discussion of this estimator). Computations were made employing the program TRANSECT (Laake et al. 1979). For calculation of the $\hat{f}(0)$ term, the perpendicular distance of each sighting was reduced by one-half the width of the exclusion area under the aircraft, where visibility was obstructed by the fuselage (total exclusion area = 530 ft at 1,000 ft ASL). This approach, in effect, moves the transect centerline outboard to the point of nearest possible sighting distance—a point where it is assumed that all animals present will be seen and counted. The question of how to deal with the problem of restricted downward visibility and line transect theory has been considered by others; however, the best treat-

[3]Holt, R. S. 1984. Testing the validity of line transect theory to estimate density of dolphin schools. U.S. Dep. Commer., NOAA Admin. Rep., NMFS-SWFC LJ-84:31, 56 p.

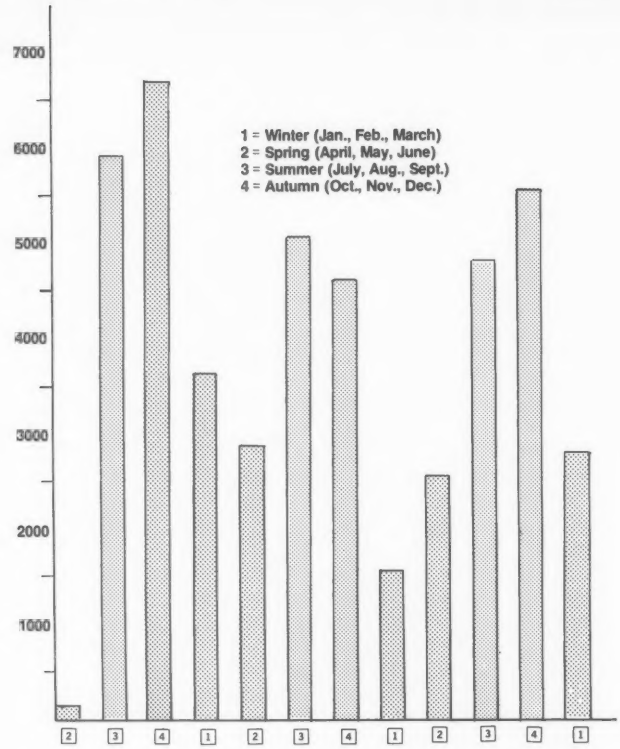

FIGURE 2.—Comparison of total counts of common dolphins on aerial surveys of the Southern California Bight by season, 1975-78.

ment of the subject, in print, is found in two papers by Leatherwood et al. (1982, 1983).

Because sample size was small in each grid-cell and in each season, data were combined to calculate a single value of $\hat{f}(0)$. The pooling of data was based on the assumption that the sightability of common dolphin groups did not vary between seasons or between regions of the surveyed area. Violation of this assumption would lead to biases in the estimates of relative densities between seasons or regions, although it would not necessarily effect mean population size estimates. The assumption of seasonal homogeneity was tested using a single classification ANOVA (two groups, unequal samples; Sokal and Rohlf 1969, p. 208). No significant difference between the distribution of perpendicular sighting distances collected in summer-autumn and winter-spring seasons was found ($F_{1,111} = 2.01$, $P = 0.18$). The same test was used to compare frequency distributions with distance of sightings collected in calmer inshore waters, with sightings collected in rougher offshore waters, since this seemed to be the most likely source of bias in sightability. No significant difference was found between the distribution of perpendicular sighting distances in the two subregions ($F_{1,108} = 1.78$, $P = 0.20$).

The rescaled frequency distribution of perpendicular sighting distance is shown in Figure 3. The probability density function, $f(x)$, is from a three-term, Fourier-series model, which provides the best fit to these data ($\chi^2 = 6.026$, df = 3, $P = 0.11$). Data were truncated at 6,600 ft in order to remove two extreme values. Intervals were specified, by inspection of the data, in order to smooth the function and minimize the effects of "heaping" in perpendicular distance measurements (Burnham et al. 1980, p. 47).

For estimation of common dolphin density (animals/km^2) in a given grid-cell for a given season, we multiplied the density of groups in a given cell

by the mean group size throughout the SCB obtained for that season. The small sample size in any cell and the very large variability in the size of groups necessitated pooling of all sightings within a season to calculate mean group size. The mean group size in summer and autumn was 338 ± 38 SE (n = 115), while that of winter and spring was 231 ± 73 SE (n = 36). While not significantly different ($F_{1,149}$ = 1.42, $P > 0.25$), we used separate mean group size in calculations of seasonal abundance. We tested the assumption that mean group size in each season was constant throughout the SCB, using a bootstrap procedure (Efron 1982). For a given season, cell i contained n_i observations of groups of mean size $\bar{s}_i$. For each cell i, we randomly drew 10,000 sets of values of size n_i from the group size distribution based on all observations recorded in that season, computed the mean of this subsample, and formed a frequency distribution of these mean values. If the percentile ranking of the observed mean group size in cell i was >97.5% or <2.5%, $\bar{s}_i$ was assumed to be a nonrandom sample. For the summer-autumn season, only 1 cell of the 26 cells containing observations of common dolphins had means which differed significantly from the rest of the surveyed area. Similarly, for the winter-spring season, only 1 cell in 10 showed a significant difference from the overall group size distribution. Therefore, group size homogeneity was assumed for these data, and a single seasonal value of mean group size ($\bar{s}$) was used in all calculations of cell density for each season.

If $\hat{f}(0)$ and $\bar{s}$ may be assumed to be homogeneous, the remaining source of between-cell variability is the density of groups. We tested the hypothesis that the density of groups is homogeneous through the SCB as follows: taking the mean number of sightings of common dolphin schools per kilometer of transect for the entire surveyed area, λ^*. We computed the expected number of cells containing a specified number of sightings of groups, using the formula:

[Expected number of cells with k sightings] =

$$\sum_{i=1}^{i=m} e^{-\lambda^* L_i} (\lambda^* L_i)^k \qquad (2)$$

where m is the total number of cells sampled, k is the specified number of sightings of groups, and L_i is the length of trackline surveyed in cell i. The expected number of cells containing k sightings were compared with the observed number for all k using a chi-square test. No significant spatial heterogeneity was evident for data collected in summer and autumn (χ^2 = 5.06, df = 5, $P > 0.5$). However, the winter and spring distribution showed clear heterogeneity in the density of groups by cell (χ^2 = 12.85, df = 3, $P < 0.005$).

We used the method of Chernoff and Moses (1959) to place confidence limits on the estimate of the number of groups per km of transect in cell i, $\hat{\lambda}_i$ (see also Clopper and Pearson 1934). We used a computer program which finds a density value, Γ_1, such that the probability of observing n_i or more groups in a transect segment of length L_i is 0.025; this is the lower confidence bound on $\hat{\lambda}_i$. Similarly, we find a density value, Γ_2, such that the probability of observing n_i or fewer groups is 0.025; this forms the upper bound on $\hat{\lambda}_i$. Γ_1 and Γ_2 are defined as satisfying the equations:

$$\sum_{k=n_i}^{k=\infty} \frac{e^{-\Gamma_1 L_i} (\Gamma_1 L_i)^k}{k!} = 0.025 \qquad (3)$$

and

$$\sum_{k=0}^{k=n_i} \frac{e^{-\Gamma_2 L_i} (\Gamma_2 L_i)^k}{k!} = 0.025. \qquad (4)$$

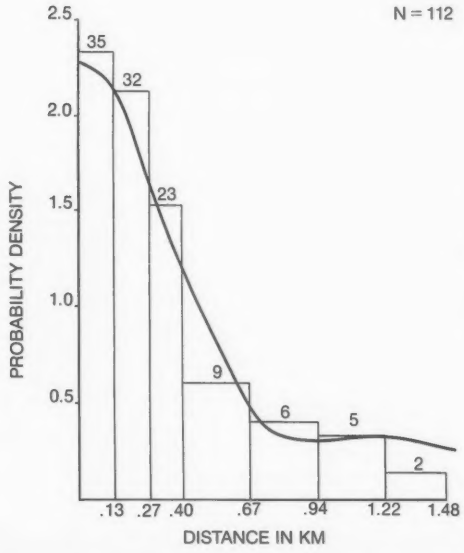

FIGURE 3.—Probability density function f(X) fit to histogram of sighting frequency and perpendicular distance (rescaled; see text).

Such confidence limits are asymmetric about $\hat{\lambda}_i$ and decrease in size with increasing transect coverage. They have the important properties that Γ_2, the upper limit, tends to be large when the transect length L_i is small, even when the number of groups observed is zero, and the lower limit Γ_1 is bounded by zero.

Population size estimates were made for each cell i in each season from the relationship $\hat{N}_i = \hat{D}_i \cdot \bar{s} \cdot A_i$, where N_i is the cell population, D_i is the estimated density of groups based on Equation (1) (groups/km^2), $\bar{s}$ is the seasonal mean group size, and A_i is the open-water area of cell i. Total population size in each season, ($\hat{N}$), was estimated as from the sum of populations in each cell, and from the theoretical formula:

$$\hat{N} = \frac{n \cdot \hat{f}(0)}{2L} \cdot \bar{s} \cdot A \qquad (5)$$

where n is the total number of groups observed, L is the total transect length, s is the seasonal mean group size, and A is the areal extent of the study area. The variance of $\hat{N}$ was estimated from the relationship (K. Burnham[4]).

$$\text{var}(\hat{N}) = A^2 \cdot \text{var}(\hat{D}_i) \qquad (6)$$

where $\text{var}(\hat{D}_i) = (\hat{D}_i)^2 \frac{\text{var}(n)}{(E(n))^2} + \frac{\text{var}(\hat{f}(0))}{(E(\hat{f}(0)))^2} + \frac{\text{var}(\bar{s})}{(E(\bar{s}))^2}$. The variance of n was calculated assuming that n had a Poisson distribution; if this assumption holds, $\text{var}(n) = n$ (Burnham et al. 1980). The variance of $\hat{f}(0)$ was calculated by program TRANSECT, using the method of Burnham et al. (1980). Variance of $\bar{s}$ was estimated as the standard error of the mean group size. The formula for variance requires that $\hat{f}(0)$ and $\bar{s}$ be independent, an assumption that may be violated due to the differen-

[4]K. Burnham, Department of Statistics, School of Physical and Mathematical Sciences, North Carolina State University, Raleigh, NC 27650-5457, pers. commun.

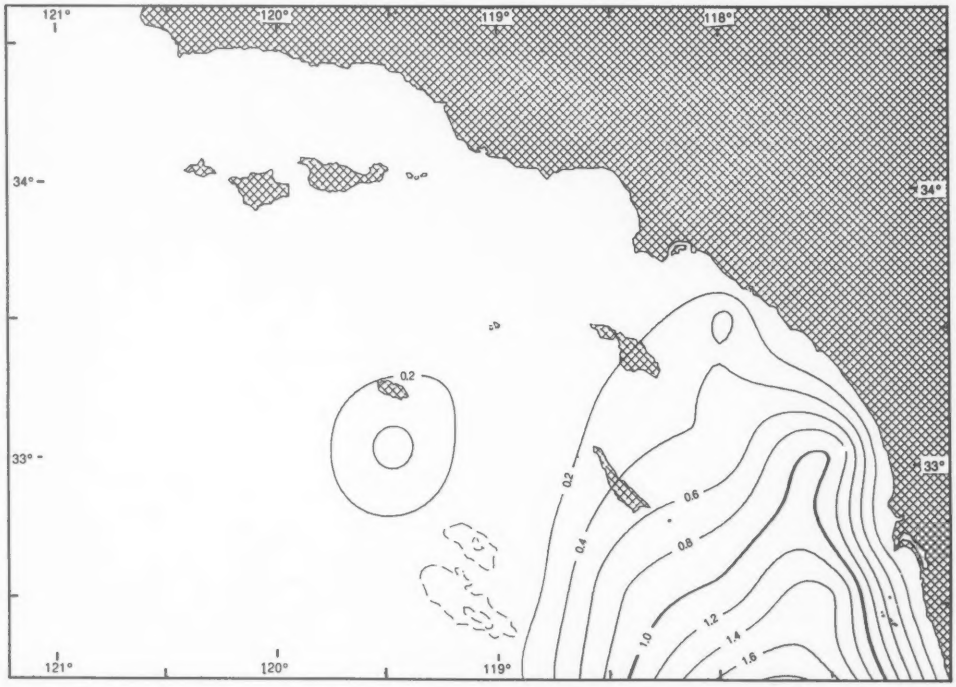

FIGURE 4.—Common dolphin distribution in the Southern California Bight, winter and spring, 1975-78. Density contours show animals/km^2.

tial sightability of large and small groups (discussed below). Because we could not be sure that the assumptions of the theoretical formula were met, we also calculated the variance of population size for the summer-autumn season, using a jackknife estimator (Miller 1974; Burnham et al. 1980). Pseudovalues of the area-wide population were generated by sequentially deleting pairs of surveys from the database. All sources of variance were considered in estimation of total variance: $\hat{f}(0)$, mean group size, and spatial variability of sightings. Because of the small number of perpendicular sighting distances for winter-spring season (31), we were unable to obtain a stable value of $\hat{f}(0)$, thus precluding the estimation of jackknife variance of that season.

Distribution maps were prepared using Surface Display Library software (Dynamic Graphics, Inc., Berkeley, CA). Contour lines, generated by linear interpolation between density values assigned to grid-cell centerpoints, were smoothed using a cubic spline function.

RESULTS

Two distinct seasonal distributions were found for common dolphins in the Southern California Bight (SCB). In winter and spring months (January through June), common dolphin sightings were almost completely confined to the eastern part of the SCB (Fig. 4). Within the area occupied, three cells in the southernmost rank and one shore-bounded cell north of San Diego showed significantly higher density than the overall seasonal mean ($P > 0.95$ in all cases). In summer and autumn months (July through December), common dolphin sightings were widespread from Rodriguez Seamount and the Patton Escarpment in the west to the mainland shore in the east (Fig. 5). Cell density estimates in this season were relatively homogeneous throughout the area. Only a single cell in the San Diego Basin could be shown to be significantly higher than the seasonal mean at the $P > 0.95$ level. Nevertheless, we believe that the clustering of moderately high-density cells east of Santa Catalina and San

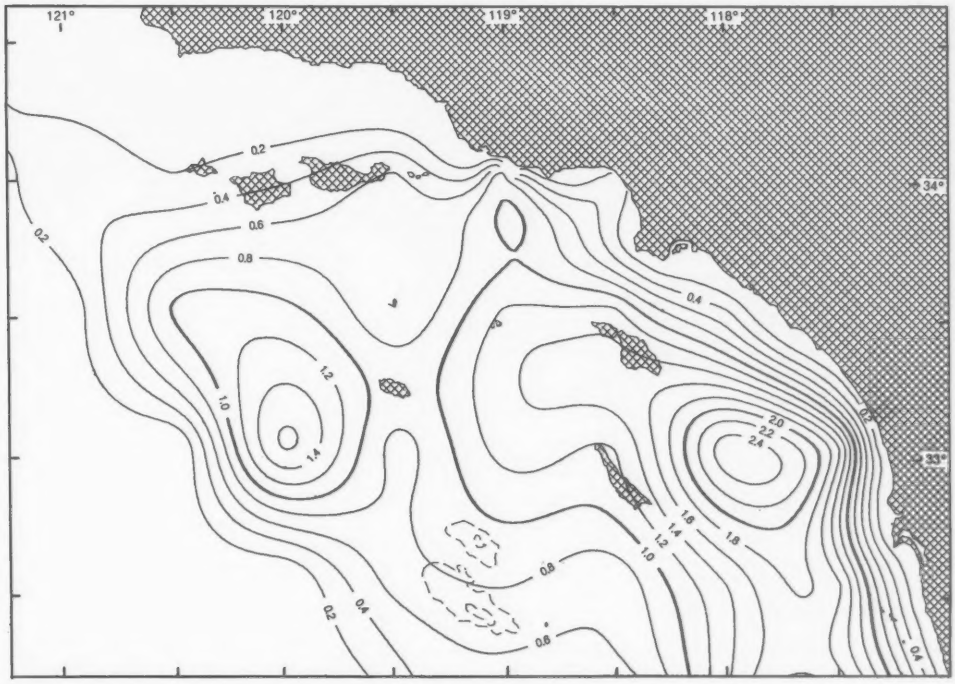

FIGURE 5.—Common dolphin distribution in the Southern California Bight, summer and fall, 1975-78. Density contours show animals/km².

Clemente Islands and west of San Nicolas Island represents a real distributional pattern.

Cell-density estimates and 95% confidence limits are provided in Tables 1 and 2. Confidence limits were calculated considering only sampling error due to number of groups sighted (Equations (3) and (4)) and not uncertainty in $\hat{f}(0)$ or mean group size. Sampling error associated with the number of groups sighted was the dominant source of variation in cell-by-cell estimates of density, typically exceeding variance of the $\hat{f}(0)$ term by three times and variance associated with mean group size by five times. It should be remembered that the density estimates are mean values computed from pooled data collected over a several month period in 3 successive years.

From these density estimates, we computed seasonal mean population size estimates. By calculating population size as the sum of the numbers in each 30′ × 30′ cell, we estimate a winter-spring population of 15,448 animals. This figure is a mean population occurring in the months of January through June and includes months of higher and lower numbers. Using Equation (5), we calculate a theoretical winter-spring population size of 18,933 animals. This second estimate for the SCB, based on pooled data, may be high because survey effort was 6.7% greater in the higher density parts of the study area in winter and spring. Based on Equation (6), the coefficient of variation of the winter-spring population was 36%. The coefficients of variation for number of groups, $\hat{f}(0)$, and mean group size were 16%, 8%, and 31%, respectively. The relatively large variability in mean group size was due to a

TABLE 1.—Relative abundance of common dolphins in the winter and spring. Mean density (animals/km²) is provided for each 30′ × 30′ cell; latitude and longitude indicate center point of cell. Upper and lower values are 95% confidence limits derived from the spatial variability of sightings along aerial transect lines.

	121°00′	120°30′	120°00′	119°30′	119°00′	118°30′	118°00′	117°30′
	7.41	1.71	1.33	2.42				
34°30′	0.00	0.00	0.00	0.00				
	0.00	0.00	0.00	0.00				
	3.42	1.05	0.81	0.62	0.86	1.28		
34°00′	0.00	0.00	0.00	0.00	0.00	0.00		
	0.00	0.00	0.00	0.00	0.00	0.00		
		5.32	1.19	0.90	1.05	0.48	1.09	1.81
33°30′		0.00	0.00	0.00	0.19	0.10	0.43	0.00
		0.00	0.00	0.00	0.05	0.00	0.19	0.00
			4.89	1.71	0.76	1.14	1.38	2.00
33°00′			0.00	0.48	0.00	0.33	0.48	0.95
			0.00	0.14	0.00	0.10	0.19	0.48
				1.24	0.71	1.95	2.57	2.80
32°30′				0.00	0.00	0.76	1.09	1.38
				0.00	0.00	0.33	0.48	0.67

TABLE 2.—Relative abundance of common dolphins in the summer and fall. Mean density (animals/km²) is provided for each 30′ × 30′ cell; latitude and longitude indicate the center point of cell. Upper and lower values are 95% confidence limits derived from the spatial variability of sightings along aerial transect lines.

	121°00′	120°30′	120°00′	119°30′	119°00′	118°30′	118°00′	117°30′
	3.53	1.45	1.32	3.12				
34°30′	0.00	0.00	0.00	0.05				
	0.00	0.00	0.00	0.14				
	1.80	1.04	1.25	1.52	2.15	2.08		
34°00′	0.35	0.21	0.35	0.62	0.83	0.35		
	0.07	0.07	0.07	0.28	0.35	0.07		
		5.82	2.70	1.73	2.70	2.15	1.25	2.56
33°30′		1.04	1.04	0.62	1.25	1.25	1.42	0.48
		0.28	0.42	0.21	0.55	0.76	0.14	0.14
			4.92	2.29	2.91	2.56	4.09	2.98
33°00′			1.66	0.76	1.32	1.25	2.56	1.66
			0.62	0.28	0.62	0.62	1.59	0.90
				2.49	2.08	1.94	3.39	3.12
32°30′				0.69	0.83	0.69	1.45	1.66
				0.21	0.35	0.21	0.62	0.90

single sighting of 2,450 animals; we choose not to treat this observation as an outlier because the occasional occurrence of very large groups is typical of this species.

For the summer-autumn season of greatest abundance, the stock size estimate based on summing individual cell populations and the estimate derived from Equation (5) were 57,270 and 46,675, respectively. The theoretical estimate based on pooled data may be low because survey effort was 7.8% greater in the lower density parts of the study area in the summer-autumn season (i.e., the offshore waters in the west). The coefficient of variation computed from the theoretical variance formula (Equation (6)) was 17%. Coefficients of variation for number of groups, $\hat{f}(0)$, and mean group size were 9%, 8%, and 11%, respectively. The jackknife estimator gave a higher coefficient of variation for population size of 27%. Components of this estimate for number of groups, $\hat{f}(0)$, and mean group size were 15%, 18%, and 14%, respectively. Differences between the two types of estimators may be due, in part, to the inherently conservative nature of the jackknife (Efron 1982), but probably result primarily from within-survey correlation of variables. In addition, the jackknife estimate of $\hat{f}(0)$ relied on a smaller subset of sighting distances measured only during summer-autumn surveys (n = 81).

DISCUSSION

Even in an area as heavily utilized as the Southern California Bight, sightings of common dolphin schools are not common events. For this reason it was necessary to pool aerial survey data collected over several months in each of three years to describe their distribution in statistical terms. The two seasonal views of common dolphin distribution in the SCB are shown for contrast in Figures 4 and 5. It is apparent that the population makes seasonally greater use of the SCB in summer and autumn months. The months of greatest numbers, based on sightings per km of trackline, were September through November. During these months, the population far exceeds the mean value of 57,000 and probably approaches 100,000 animals.

A potential source of bias in our mean population size estimates was the differential sightability of groups of various sizes. The detection function for common dolphin sightings declined sharply beyond about 1,650 ft (500 m), suggesting that mostly large or conspicuous groups were seen at relatively great distances. The Fourier estimator is robust to variation in sighting efficiency (Burnham et al. 1980). For comparison, the $\hat{f}(0)$ term of 2.29 for common dolphins was quite close to the $\hat{f}(0)$ estimate of 2.16 more recently obtained for 136 sightings of Pacific white-sided dolphin schools on aerial surveys offshore of central and northern California (Dohl et al. 1983). However, variable sighting effectiveness may also bias the estimation of mean group size. Holt and Powers (1982) found that smaller groups of dolphins were more likely to be missed on aerial surveys than larger groups, resulting in a 25% overestimation of mean group size. For our data on common dolphins, we did not find a significant difference in mean group size between sightings within the first 1,650 ft and beyond due to high variability in sightings size (213 $\pm$ 46 SE, n = 65, compared with 308 $\pm$ 49 SE, n = 50; $F_{1,113}$ = 1.94, P = 0.18). Nevertheless, our calculations show that stratification of mean group size by distance from the trackline (<1,650 ft and >1,650 ft) would result in an 18% decrease in mean density values.

The distribution shown for summer and autumn can be viewed as a composite of monthly distributions. Common dolphin distribution expands from the southeast into the central and western parts of the SCB in late spring and early summer and recedes toward the east and south in late autumn and early winter. Common dolphin movement into and out of the SCB appears to be temperature related. As sea surface temperatures (SST) rise in late spring-early summer, animals begin to be sighted more often along the Coronado Escarpment. Peak numbers of common dolphins were found in open water regions of the SCB 3-5 wk after intrusion of the warmer waters. During cool-water months, when SSTs down to 10.0°C were recorded and the SCB-wide mean was 14.6°C, no animals were observed in waters cooler than 14.0°C.

Distributional patterns of the common dolphin within the SCB may be changing. Hui (1979) analyzed data collected on Naval Ocean Systems Center (NOSC) surveys from 1968 through 1976 and showed no common dolphin sightings north of Point Vincente (lat. 33°45'N) or west of approximately San Nicolas Island. Our surveys in summer and autumn months found 29.9% of all sightings and 30.8% of all animals occurred in the northern and western portion of the SCB—an area largely unsampled by the NOSC surveys. Hui's results agreed with those of Evan's (1975), who found only a small fraction of the total sightings recorded on aerial and shipboard surveys to occur in this northern and western portion of the SCB; however, aerial sampling effort in Evan's earlier study also favored the inshore and southern portions of the SCB.

Based upon the distribution of sightings on our bimonthly aerial surveys, movement of common dolphins into the SCB appeared to follow the network of escarpments and seamounts noted by Evans (1971). The major corridor was along the Coronado Escarpment to Thirty-Mile Bank, up to the Catalina Escarpment, around both sides of Santa Catalina Island, along the western margins of the San Pedro and Santa Monica basins to Santa Cruz and Santa Rosa Islands (Fig. 1). The population front then advanced westward along the southern margin of these islands until reaching the Santa Rosa-Cortés Ridge where it shifted south, spreading out along the western slope of this prominant underwater feature. Some elements of this influx stopped and along the way, increasing summer-autumn populations significantly in the San Pedro Channel, Gulf of Santa Catalina, and, to a lesser extent, in nearshore waters from Dana Point to La Jolla. A secondary pathway was from Forty-Mile Bank in the south, up the San Clemente Escarpment west of San Clemente Island to reach the Santa Rosa-Cortés Ridge area.

During periods of peak occupancy common dolphin sightings west of long. 119°W were distributed along the western slope of the Santa Rose-Cortés Ridge centered at lat. 33°00′N, long. 120°00′W. As waters cooled, the distributional center shifted eastward to locate over the eastern slope of the Santa Rosa-Cortés Ridge at 33°00′N, 119°20′W, while a smaller element moved northwesterly to a new location around 33°30′N, 120°30′W. With continued cooling of the western waters, the majority of the animals along the eastern edge of the Ridge appeared to move southeasterly to merge with existent populations south and east of San Clemente Island. The remaining small number of animals wintering-over moved westward, centering near 33°00′N, 119°30′W, south of San Nicolas Island.

The destination of common dolphins that moved northwesterly from the summering grounds over the western edge of the Santa Rosa-Cortés Ridge is unknown. However, several pieces of incomplete evidence lead us to believe that they are part of a "pelagic" population that returns in late autumn or early winter to offshore waters over the Rodriguez Seamount or Patton Escarpment. During several midsummer ship surveys and three aerial surveys of offshore waters over the Patton Escarpment and San Juan Seamount, we recorded sightings of large schools of robust-bodied, brilliantly marked, "pelagic" common dolphins. On two occasions, our crew on the catch boat head-netted, brought on board, photographed, measured, tagged, freeze-branded, and released, examples of these "pelagic" animals from within schools containing predominantly the paler, smaller, nearshore variety of *Delphinus*. Ships' logs indicate that the presence of these "pelagic" animals increased with distance from shore, and percentages as high as 50% were found in mixed schools of common dolphins at the western boundary of catch trips, usually south of lat. 33°45′N and west of long. 120°00′W. West of the Patton Escarpment, mixed schools were not noted, and the few schools encountered contained only "pelagic" animals (Dohl unpubl. data).

In summary, this study establishes an extended distributional range of the common dolphin within the SCB, identifies areas of significantly greater seasonal use, and provides seasonal mean population estimates. Our results confirm the findings of earlier studies that common dolphins move into the SCB following major features of underwater topography in response to increasing seasonal water temperatures. Observations on surveys also seem to indicate that most of the population moves through the SCB in a generalized counterclockwise direction, and that the western summer-autumn population is augmented by an influx of "pelagic" animals from far offshore.

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CETACEAN HIGH-USE HABITATS OF THE NORTHEAST UNITED STATES CONTINENTAL SHELF[1]

ROBERT D. KENNEY AND HOWARD E. WINN[2]

ABSTRACT

Results of the Cetacean and Turtle Assessment Program previously demonstrated at a qualitative level that specific areas of the continental shelf waters off the northeastern U.S. coast consistently showed high-density utilization by several cetacean species. We have quantified, on a multispecies basis and with adjustment for level of survey effort, the intensity of habitat use by whales and dolphins, and defined areas of expecially high-intensity utilization. The results demonstrate that the area off the northeast United States, which is used most intensively as cetacean habitat, is the western margin of the Gulf of Maine, from the Great South Channel to Stellwagen Bank and Jeffreys Ledge. Secondary high-use areas include the continental shelf edge and the region around the eastern end of Georges Bank. High-use areas for piscivorous cetaceans are concentrated mainly in the western Gulf of Maine and secondarily at mid-shelf east of the Chesapeake region, for planktivores in the western Gulf of Maine and the southwestern and eastern portions of Georges Bank, and for teuthivores along the edge of the shelf. In general, habitat use by cetaceans is highest in spring and summer, and lowest in fall and winter.

From October 1978 through January 1982, the Cetacean and Turtle Assessment Program (CETAP) at the University of Rhode Island conducted surveys of the waters of the U.S. continental shelf from Cape Hatteras, NC, to the northern Gulf of Maine. The purpose of these surveys was to provide data on the distribution and abundance of whales, dolphins, and sea turtles inhabiting the northeast shelf for input to decision-making relative to offshore oil and gas resource development. Twenty-six species of cetaceans were observed during the study, and their distributions have been described in some detail (CETAP 1982). Each species exhibited a distinctive pattern of distribution in space and time, inhabiting some small portion(s) of the study area at higher relative densities.

When comparing distributions of individual species, there appear to be specific geographic areas which consistently contained higher abundances of several cetacean species. This phenomenon had been noted during the CETAP study (CETAP 1982), but had not been analyzed quantitatively. An individual species approach to the analysis of such multispecies phenomena has certain limitations. One cannot simply combine the sighting distributions of several species; the different cetacean species vary widely in size and may have quite different ecological requirements. An additional complication in a study of habitat use, based on sighting data, is introduced by the uneven allocation of sighting effort. One cannot be certain whether a lack of sightings is due to absence of whales or absence of observers, or, conversely, whether a concentration of sightings represents a real concentration of whales or simply a concentration of effort. Thus it is difficult to simply or directly combine single-species sighting distributions in any sort of multispecies habitat use analysis. In this paper, we have attempted to synthesize, from the CETAP individual species sighting data, a measure of the intensity of habitat use by the total cetacean fauna in the study area which accounts for both interspecific differences and differences in allocation of effort. These results then serve to delineate those specific habitat areas which are used at particularly high levels by whales and dolphins off the northeastern United States.

An underlying assumption in this paper is that a habitat which is occupied by whales or dolphins is necessarily utilized by them. Previous results from CETAP data have shown that the distribution of sightings of a particular species where definite feeding behavior was observed tended to closely mirror the overall sighting distribution for that species. Only feeding activity at or very near the surface can be seen by observers on ships or airplanes, but much feeding behavior likely occurs below the surface. For some species, observations of surface feeding are very rare. In addition, cetaceans are large mammals

[1]This report has been reviewed by the Minerals Management Service and approved for publication. Approval does not signify that the contents necessarily reflect the views and policies of the Service, nor does mention of trade names or commercial products constitute endorsement or recommendation for use.

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with high metabolic rates and accordingly high feeding rates. They are estimated to consume prey equivalent to 1.5-4% of their body weight daily (Sergeant 1969; Lockyer 1981), with some estimates for smaller species as much as 10% of body weight per day (e.g., Smith and Gaskin 1974). The CETAP study concluded that cetaceans "would be expected to feed virtually every day while in the study area" and that "each species of cetacean was likely feeding, either at the surface or below, in any area in which it was seen regularly" (CETAP 1982, p. 417). For the purposes of the current study, we have also followed this reasoning and assumed that a habitat which is being occupied by one or more cetacean species is therefore being utilized by those species as a feeding area.

METHODS

The CETAP study area was defined as the waters of the U.S. continental shelf north of Cape Hatteras, from the shoreline to 5 nmi (9.3 km) seaward of the 1,000 fathom (1,829 m) isobath. Surveys were conducted from October 1978 through January 1982. Data collected from two types of surveys have been used in this analysis:

1) *Dedicated aerial surveys*: Random transect aerial surveys were conducted in defined blocks within the study area, including both regular surveys throughout the year and special surveys targeted at endangered species, particularly right whales. The primary objective of these surveys was to estimate the absolute abundance, e.g., the total number of individuals in the population, of each species in the study area, using line transect census methods (Burnham et al. 1980; Scott and Gilbert 1982). This methodology requires consistent use of rigorously standardized sampling, e.g., use of the same platform, even allocation of sampling across the different blocks, and random selection of transects within a block.

The two aircraft used for these surveys were a Beechcraft[3] AT-11 and a Cessna 337-G Skymaster, both twin-engine planes. The AT-11 crew consisted of a pilot, a navigator, and four observers; two observers at a time were stationed in a clear acrylic observation bubble in the nose of the plane. The Skymaster carried a pilot, a navigator, and two observers, who sat in the rear seats and watched out the side windows. All surveys were conducted at an altitude of 750 ft (229 m) and a groundspeed of 120 kn (222 km/h).

For any particular survey, a series of parallel track lines was flown. For the regular surveys, the lines sampled were randomly chosen from a pool of lines running northwest-southeast (roughly perpendicular to the bathymetry) and spaced at 2 nmi intervals throughout the block to be sampled. For the endangered species surveys, the lines were systematically spaced at a predetermined interval, with the first line placed at a randomly determined distance from the edge of the block.

2) *Platforms of opportunity (POP) surveys*: Trained observers were placed aboard various ships and aircraft operating within the study area in order to collect distributional data to supplement the dedicated surveys. The platforms most often used included Coast Guard cutters, U.S. and foreign oceanographic and fisheries research vessels, and Coast Guard fisheries patrol and thermography aircraft. The track of the ship or aircraft was wholly determined by its primary mission. These data could not be used in abundance estimation because effort was not allocated randomly or evenly, and the platforms used were not exactly comparable.

Observers on both types of surveys recorded a variety of information. The data collected included date, time, latitude and longitude, platform heading, beginning and end of periods when the observer(s) were actively on watch, and environmental information (air temperature, water temperature, depth, weather, visibility, sea state, wind direction, and cloud cover). The data were recorded at each sighting, as well as at periodic intervals (typically 5 min for aerial and 30 min for shipboard surveys) during all on-watch periods. This allowed for subsequent reconstruction of flight-cruise tracks. Additional data recorded at sightings included species, reliability of identification, number of animals, distance from the platform, animal heading, and behaviors.

The data were transcribed from the field forms to coding forms, keypunched, and input to a computer data base. A number of quality control steps were included in the process, and all discovered errors were corrected. In addition to the two types of survey data described above, historical sighting data collected prior to CETAP and opportunistic sighting data provided by fisherman, mariners, whalewatchers, fish-spotters, pilots, etc. are included in the CETAP data. None of these data have associated track-line information, and are therefore not included in this paper. After completion of the CETAP

[3]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

study, the entire data base was archived on magnetic tape at the University of Rhode Island Academic Computer Center. The data base is very large, comprising nearly 70,000 entries and 112 variables; it includes almost 25,000 sightings of cetaceans, sea turtles, or other large marine animals (e.g., sharks, ocean sunfish, swordfish, rays, etc.).

For this paper, the study area was partitioned into blocks measuring 10 minutes of latitude by 10 minutes of longitude. The area of the blocks ranges from about 243 km^2 at the northern extreme of the study area to about 281 km^2 at the southern end, due to the curvature of the earth's surface and resulting convergence of the meridians toward the north pole. The data were further grouped by calendar seasons across all the years of sampling. All dedicated aerial and POP data which met defined criteria were included in the analysis. These criteria included observer(s) formally on watch, clear visibility of at least 2 miles, and sea states of Beaufort 3 or lower. Although the dedicated aerial and POP data were not directly compatible for the purpose of absolute abundance estimation, we are justified in combining them for this analysis. An examination of sighting effort in the 1979 CETAP data (Hain et al. 1981) demonstrated a significant correlation between numbers of sightings and length of line surveyed for both aerial and POP surveys. Reanalysis of these same data shows that the average number of sightings per mile of track line surveyed was somewhat higher for the POP surveys, but that the difference is not statistically significant at the 5% level (paired Student's *t*-test). Since we are in effect using the number of sightings per unit length of track line as a measure of relative abundance in this analysis, the two data types can be combined.

To remove any bias due to uneven allocation of sighting effort among the blocks, the effort was first quantified. A computer program was developed which calculated the length of track line surveyed each season within each of the 10-minute blocks, including only line segments surveyed within the criteria defined above. Each line surveyed is recorded in the data base as a sequence of latitude-longitude positions. For any pair of successive positions, the length of track line between the points (D, in km) can be calculated by:

$$D = 111.12 \arccos [\sin (X_1) \sin (X_2) + \cos (X_1) \cos (X_2) \cos (Y_2 - Y_1)],$$

where X_1 and X_2 are the latitudes of the two positions, and Y_1 and Y_2 are the corresponding longitudes. This calculates great circle distance. Flight or cruise tracks would actually be rhumb lines rather than great circles, but the algorithm required to calculate rhumb line distance is much more complex. Furthermore, for two points around 10 km apart, typical of track line segments in the data, great circle and rhumb line distance differ by <1 m, an error of <0.01%.

For a pair of points within a single 10-minute block, the length of the intervening line segment is simply assigned to that block. The difficulty arises for successive points located in separate blocks. It is then necessary to find the point(s) of intersection where the track line crosses any block boundary(ies). The bulk of the computer program is concerned with this procedure. For a pair of points in separate blocks, the equation describing the great circle through the points is defined. The point where that line crosses a boundary is then determined by inserting the latitude or longitude value defining the boundary into the great circle equation, and then solving for the other coordinate. The line segment which originally spanned two or more blocks is thereby partitioned into smaller segments, each wholly contained in a single block, whose lengths are then calculated as above. The final step in the procedure is to sum the lengths of all the line segments within the block, which represents the amount of sighting effort expended in the block.

All cetacean sightings made during track segments meeting the defined criteria were also extracted from the data base. These data were summarized to produce, for each species, the total number of individual animals sighted in each block and season. (This is not to say that this number represents all different individuals. An individual may be sighted repeatedly by different surveys, but this is taken into account by the correction for effort.) In order to combine different species, the number of animals of a particular species was multiplied by the species' estimated average body weight to calculate biomass sighted per block and season. The biomass data for each species were then partitioned into three feeding classes—piscivorous, teuthivorous, and planktivorous—based upon the estimated percentages of each species' diet composed of fish, squid, and zooplankton, respectively. In an earlier analysis of prey consumption by cetaceans in the CETAP study area, Scott et al.[4] classified each species into a single category based on its principal prey type;

[4]Scott, G. P., R. D. Kenney, T. J. Thompson, and H. E. Winn. 1983. Functional roles and ecological impacts of the cetacean community in the waters of the northeastern U.S. continental shelf. Paper presented at 1983 annual meeting, International Council for the Exploration of the Sea, ICES C.M. 1983/N:12.

however, we felt that using the estimated proportion of the diet comprised of the different prey types was a more realistic representation of what was actually occurring in the ecosystem. The body weight and prey preference estimates were taken from Kenney et al. (1985), who had based their estimates on an extensive literature review. For three species not included in that reference—beluga, false killer whale, and rough-toothed dolphin—body weight and prey preference estimates were based on Watson (1981) and Nishiwaki (1972). For the categories of sightings which were not completely identified, the body weight and prey percentages were calculated as averages for all species included in the category and weighted by the number of sightings of each. (It might be argued that the unidentified categories should be excluded totally and that their inclusion introduces too much uncertainty. However, we felt that excluding them would eliminate many potentially valuable observations and that including them would provide a closer measure of habitat use. Some of the categories can be narrowed to only a couple of species, and the number of sightings overall is a valid basis for estimating the probability of an unidentified sighting being a particular species.)

The biomass data were then summed for all species in each block and season, as well as for the piscivorous, teuthivorous, and planktivorous subsets. Values for endangered species biomass were also calculated by summing the data for right, humpback, blue, fin, sei, and sperm whales, as well as for the estimated proportion of the unidentified categories made up of these species. The biomass data for each block and season were then divided by the corresponding effort data, resulting in values of biomass per unit effort (BPUE) in units of kilograms of cetacean sighted per kilometer of track line surveyed (kg/km). The final data set therefore had, for each block, BPUE values for all cetaceans, for endangered species only, and for the piscivorous, teuthivorous, and planktivorous components of the cetacean fauna for each season and for the entire year.

The simplest technique for looking at the pattern of high-intensity habitat use by cetaceans is to plot the blocks with the highest values of BPUE. Obviously, the blocks with the highest BPUE values within any of the individual data sets are those with the highest intensity of habitat use. The question becomes one of defining the cutoff point in each distribution for selecting the highest values. The frequency distributions of each of the BPUE data sets were examined for any patterns which might be useful as an objective criterion to define a lower bound for the high-use blocks (e.g., bimodal distributions, or 2 standard deviations above the mean of a normal distribution). Log-survivorship plots (plotting BPUE vs. log of the number of blocks with higher BPUE values; see Fagen and Young 1978) were also tried to look for changes in slope which could serve as a means of numerically defining this boundary. When these techniques failed to select any specific value for the cutoff point, we opted to use simple percentile rankings to classify the blocks for plotting the results.

The final step in the analysis was to develop an index which would serve to define those areas which are most important as cetacean habitat. By "important" we include both the level of habitat use and the management priority of the individual species. Habitat requirements for an individual probably depend heavily upon prey type, so each of the data sets for the three feeding classes were included in this process. Since management objectives concentrate on the endangered species, the endangered species data sets were also included. Since the endangered species data are also part of the feeding type data, the former are in effect being included twice. This gives the endangered species extra weight in the index, in accord with both their endangered status and management focus. For each seasonal set of BPUE data for the endangered species and the three feeding classes, blocks were assigned points as follows: 5 if the BPUE was greater than the 99th percentile value for that data set, 3 if it was between the 95th and 99th percentiles, 1 if between the 90th and 95th percentiles, and 0 otherwise. The value of the index for a block is then the sum of these point values for all data sets. Since there were four seasons and four BPUE variables used, the maximum possible value for the index in any block would be 80 ($4 \times 4 \times 5$). For lack of a more concise term, we shall refer to this as Habitat Use Index, although it does have the additional dimension of focus on endangered species. Since this index is based on only the top 10% of each of the 16 individual data sets, it provides a simple way to point out those blocks which repeatedly stand out as high-use habitat in more than one season and/or for more than one prey type.

RESULTS

During the CETAP study, observers on dedicated aerial or POP surveys operating within the defined survey criteria made 5,304 sightings of 26 different species of whales and dolphins. These include sighting of individuals in three genera—*Globicephala*, *Mesoplodon*, and *Kogia*—which could only be iden-

tified in the field to genus. In addition, there were 2,039 sightings of 30 more or less unidentified categories of cetaceans, bringing the grand total to 7,343 sightings. Table 1 lists all the observed cetacean species and unidentified categories, with numbers of sightings of each. It also shows, for each species, the values used in this analysis for estimated average body weight and percentage of diet comprised of the three major prey types.

Overall, 1,476 10-minute blocks were sampled by CETAP dedicated and POP surveys, with a total of over 373,000 km of track line surveyed within acceptable criteria. Somewhat fewer blocks were sampled during any one season. Sighting effort was most in-

TABLE 1.—List of cetacean species and unidentified categories sighted by CETAP dedicated aerial and POP surveys on the northeast U.S. shelf, showing number of sightings, estimated body weight, and estimated percentage of the diet comprised of fish, squid, and zooplankton. Endangered species are identified by *.

Species or category	No. of sightings	Body weight (kg)	Percent of diet		
			Fish	Squid	Zooplankton
Right whale, *Balaena glacialis**	173	40,000	0	0	100
Humpback whale, *Megaptera novaeangliae**	409	25,000	95	0	5
Sperm whale, *Physeter catodon**	258	20,000	20	80	0
Blue whale, *Balaenoptera musculus**	2	70,000	0	0	100
Fin whale, *B. physalus**	946	30,000	90	0	10
Sei whale, *B. borealis**	62	13,000	0	0	100
Minke whale, *B. acutorostrata*	215	4,500	95	0	5
Beaked whale, *Mesoplodon* sp.	11	1,200	0	100	0
Goosebeaked whale, *Ziphius cavirostris*	4	1,900	0	100	0
Northern bottlenose whale, *Hyperoodon ampullatus*	4	4,700	5	95	0
Beluga whale, *Delphinapterus leucas*	1	420	100	0	0
Pygmy/dwarf sperm whale, *Kogia* sp.	1	300	0	100	0
Pilot whale, *Globicephala* sp.	537	850	0	100	0
Killer whale, *Orcinus orca*	4	3,000	90	10	0
False killer whale, *Pseudorca crassidens*	1	500	50	50	0
Pygmy killer whale, *Feresa attenuata*	1	150	100	0	0
Gray grampus, *Grampus griseus*	421	340	0	100	0
Bottlenose dolphin, *Tursiops truncatus*	828	150	100	0	0
White-beaked dolphin *Lagenorhynchus albirostris*	10	150	50	50	0
Atlantic white-sided dolphin, *L. acutus*	374	120	90	10	0
Rough-toothed dolphin, *Steno bredanensis*	1	100	50	50	0
Saddleback dolphin, *Delphinus delphis*	340	65	85	15	0
Striped dolphin, *Stenella coeruleoalba*	63	55	40	60	0
Spotted dolphin, *S. attenuata* or *plagiodon*	51	50	20	80	0
Spinner dolphin, *S. longirostris*	3	50	20	80	0
Harbor porpoise, *Phocoena phocoena*	584	45	95	5	0
Unidentified (unid.) whale	263	25,000	71	12	17
Unid. large whale	139	27,900	70	11	19
Unid. large whale, not *B. glacialis*	2	26,700	77	12	11
Unid. large whale, not *P. catodon*	5	29,200	78	0	22
Unid. rorqual	30	24,800	88	0	12
Unid. rorqual, not *B. acutorostrata*	62	27,900	87	0	13
Unid. rorqual, not *M. novaeangliae*	6	24,800	86	0	14
P. catodon or *M. novaeangliae*	2	23,100	66	31	3
P. catodon, *M. novaeangliae*, or *B. glacialis*	6	26,600	52	25	23
B. musculus, *physalus*, or *borealis*	127	29,000	84	0	16
Unid. medium whale	68	4,080	81	15	4
Unid. beaked whale	19	2,090	1	99	0
Unid. beaked whale or *P. catodon*	2	17,600	18	72	0
Mesoplodon sp. or *Z. cavirostris*	2	1,390	0	100	0
Unid. blackfish	4	863	1	99	0
Unid. large blackfish	1	864	1	99	0
Globicephala sp. or *P. crassidens*	6	849	0	100	0
Unid. dolphin	785	133	74	26	0
Unid. beaked dolphin	120	117	85	15	0
Unid. dolphin, not *G. griseus*	161	96.7	90	10	0
Unid. long-beaked dolphin	11	112	84	16	0
Lagenorhynchus sp.	10	121	89	11	0
Lagenorhynchus sp. or *T. truncatus*	2	141	96	4	0
L. acutus or *D. delphis*	23	93.8	88	12	0
Stenella sp.	86	52.7	31	69	0
Stenella sp., not *S. longirostris*	64	52.8	31	69	0
Stenella sp. or *T. truncatus*	8	126	83	17	0
S. coeruleoalba or *T. truncatus*	1	136	91	9	0
S. attenuata/plagiodon or *T. truncatus*	3	138	90	10	0
Stenella sp. or *D. delphis*	21	59.6	61	39	0

tense during spring, followed in descending order by summer, fall, and winter. Table 2 summarizes the sighting effort by season and for the entire year.

The BPUE data are summarized in Table 3. The distributions of BPUE values for all categories and seasons were very similar. Each distribution was highly skewed toward lower values. This can be seen from the table; mean values ranged between 33 and 423 kg/km, but maximum values were as high as 33,747 kg/km. In 20 of the 25 cases, the median value was 0, and in 9 of these the 75th percentile value was also 0, indicating that no cetaceans of that particular category were seen in one-half or three-quarters, respectively, of the blocks surveyed. In fact, in two cases (endangered species and planktivores sighted in winter) even the 90th percentile value was 0; no endangered or plankton-feeding cetaceans were observed in 9 out of 10 blocks surveyed in the winter.

The overall pattern of high habitat use by cetaceans is depicted in Figure 1, which shows those 10-minute blocks with the top 10% of the whole-year BPUE values (all species combined). The figure also identifies locations to be used for geographic reference. Three principle high-use areas can be delineated: 1) the western margin of the Gulf of Maine, from the Great South Channel northward to Jeffreys Ledge, 2) the eastern portions of Georges Bank, along with the Northeast Channel and relatively deep basin north of the bank, and 3) the continental shelf edge. There are also scattered high-use blocks in other areas.

TABLE 2.—Summary of sighting effort in 10-minute blocks, expressed as kilometers of track line surveyed within acceptable criteria, for CETAP dedicated and POP surveys.

	Season				
	Winter	Spring	Summer	Fall	Total
Blocks sampled	1,179	1,344	1,395	1,169	1,476
Mean effort per block	40.3	108.0	80.7	58.2	252.9
Standard deviation	32.9	104.9	56.1	47.6	207.9
Maximum effort per block	372	1,137	596	546	2,389
Total effort	47,506	145,204	112,576	67,994	373,280

TABLE 3.—Mean, median, and maximum values of biomass sighted per unit of sighting effort, by season and for the entire year, for all cetacean species combined, endangered species only, and fish-, squid-, and plankton-feeding cetaceans.

		Biomass per unit effort (kg/km)		
Cetacean category	Season	Mean	Median	Maximum
All cetaceans	All	368	67	15,170
All cetaceans	Winter	234	[1]0	23,049
All cetaceans	Spring	423	2	20,928
All cetaceans	Summer	386	0	28,447
All cetaceans	Fall	270	0	33,747
Endangered species	All	296	0	15,170
Endangered species	Winter	198	[1,2]0	22,048
Endangered species	Spring	350	0	20,268
Endangered species	Summer	323	[1]0	27,478
Endangered species	Fall	190	[1]0	33,072
Piscivores	All	205	21	6,920
Piscivores	Winter	139	[1]0	16,266
Piscivores	Spring	256	1	15,446
Piscivores	Summer	235	0	22,483
Piscivores	Fall	158	0	23,995
Teuthivores	All	83	1	4,249
Teuthivores	Winter	62	[1]0	11,879
Teuthivores	Spring	80	0	3,582
Teuthivores	Summer	83	0	5,380
Teuthivores	Fall	79	0	5,625
Planktivores	All	80	0	12,323
Planktivores	Winter	33	[1,2]0	8,190
Planktivores	Spring	87	0	5,874
Planktivores	Summer	68	[1]0	12,910
Planktivores	Fall	33	[1]0	5,805

[1]75th percentile value was also 0.
[2]90th percentile value was also 0.

Figure 2 shows the patterns of high habitat use, again as the upper 10% of BPUE values, for the entire cetacean community in each of the four seasons. The seasonal patterns do not show any major differences; however, a slight north-south shift in the pattern is evident. The number of high-use blocks is higher in the northern portion of the area and lower in the southern portion during spring and summer than during fall and winter. It should be emphasized that the plots in Figure 2 do not indicate differences in magnitude of utilization intensity between seasons, but only pattern differences. Since the blocks which are plotted are the upper 10% of the BPUE values for each seasonal distribution, the numbers of blocks plotted for each season are fairly equivalent. For example, it appears from the plots that the shelf edge may be more intensely used in the winter than during the other seasons, but actually the reverse is true. It is simply that the blocks with highest winter utilization tend to be on the shelf edge, but the intensity of use in these blocks is still lower. Seasonal differences in intensity of habitat use can be seen by referring back to Table 3. The intensity of habitat use is highest in the spring and second highest in the summer for all categories except the teuthivores, where the summer utilization is most intense and spring and fall very close behind. There

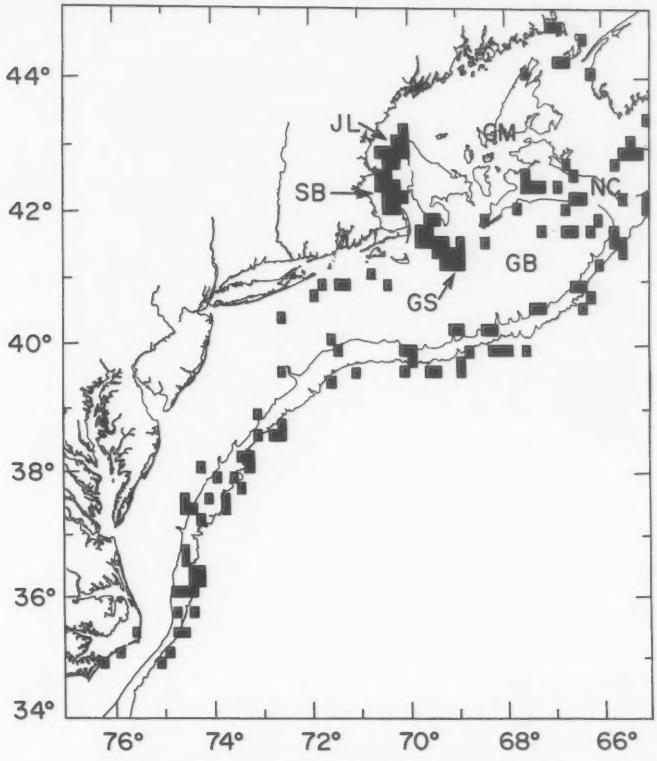

FIGURE 1.—Plot of 10-minute blocks with total cetacean biomass per unit effort values in the top 10% of all blocks. GM = Gulf of Maine; GB = Georges Bank; NC = Northeast Channel; JL = Jeffreys Ledge; SB = Stellwagen Bank; GS = Great South Channel.

is a general pattern of reduced utilization during the fall and winter.

Figure 3 shows the whole-year patterns of high habitat usage for the four subsets of the total cetacean community. The pattern for endangered species shows only slight differences from the total community pattern seen in Figure 1. Differences from the total community pattern become somewhat greater in the piscivorous component. The intensity of utilization along the shelf edge is less, but there appears an area or areas of high use at midshelf east of the Chesapeake Bay region. The planktivorous component shows a distinctive pattern. There are only scattered high-use blocks in the southern half of the area. In the northern half of the area, the pattern is similar to those for the entire community, endangered species, or piscivores, except that there are more high-use blocks in the central portion of the Gulf of Maine and on the southern part of Georges Bank. The teuthivorous component shows the most distinct pattern, with a dense concentration of high-use blocks along the shelf edge in the southern half of the area and a less dense concentration along the more northern shelf edge and in the vicinity of the Northeast Channel.

Finally, Figure 4 presents the overall composite pattern of high-use areas, plotting those 10-minute blocks with Habitat Use Index values in the upper 5%, 10%, and 20% of all blocks sampled. Of the total of 1,476 blocks surveyed, 889 had index values of 0 and 587 were 1 or greater. The maximum index value was 49 for a block located at the northern end of Stellwagen Bank. Table 4 lists the blocks in the upper 1% of the distribution, showing their locations. Of those 16 blocks, 13 are in the western Gulf of Maine between the Great South Channel and Jeffreys Ledge. This area shows the densest concentration of high-use blocks in Figure 4. The secondary

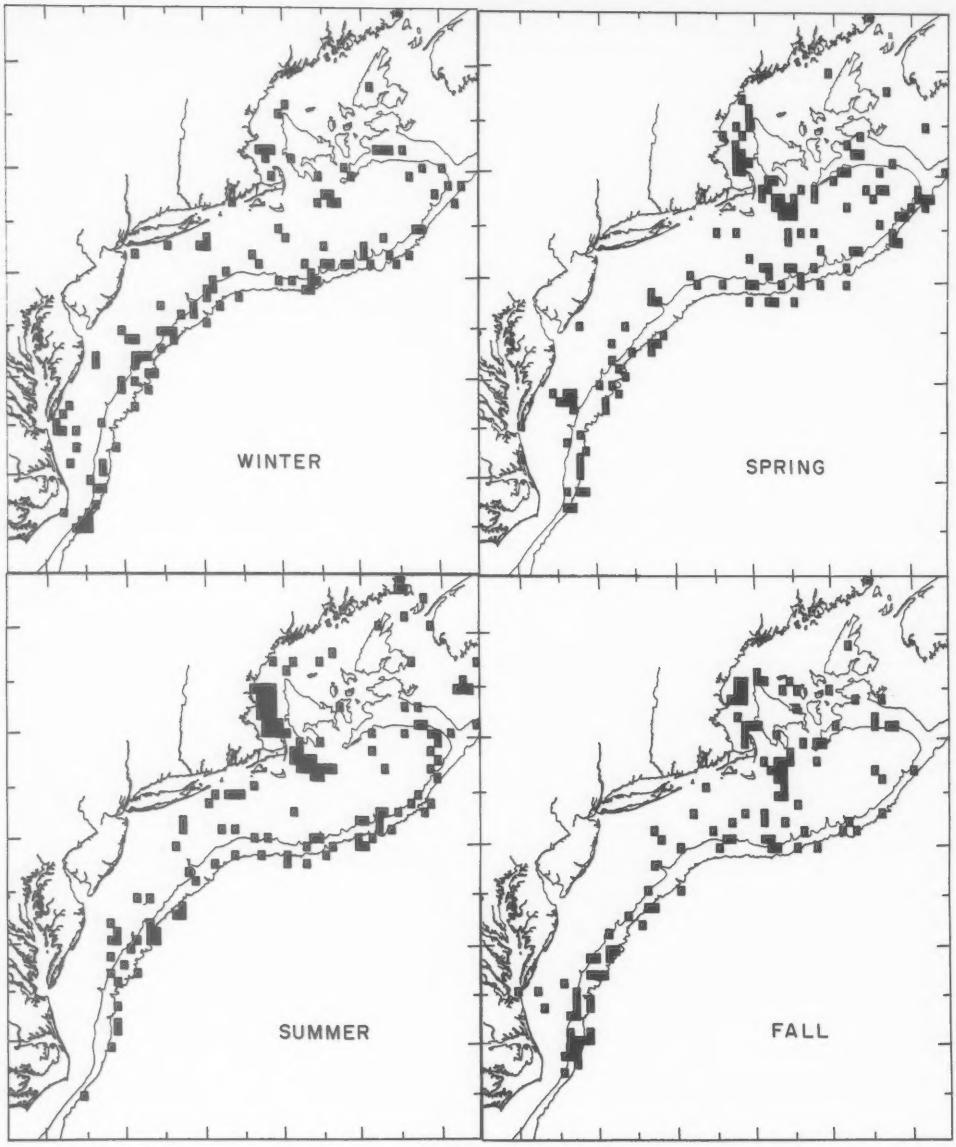

FIGURE 2.—Seasonal patterns of the top 10% of total cetacean biomass per unit effort values.

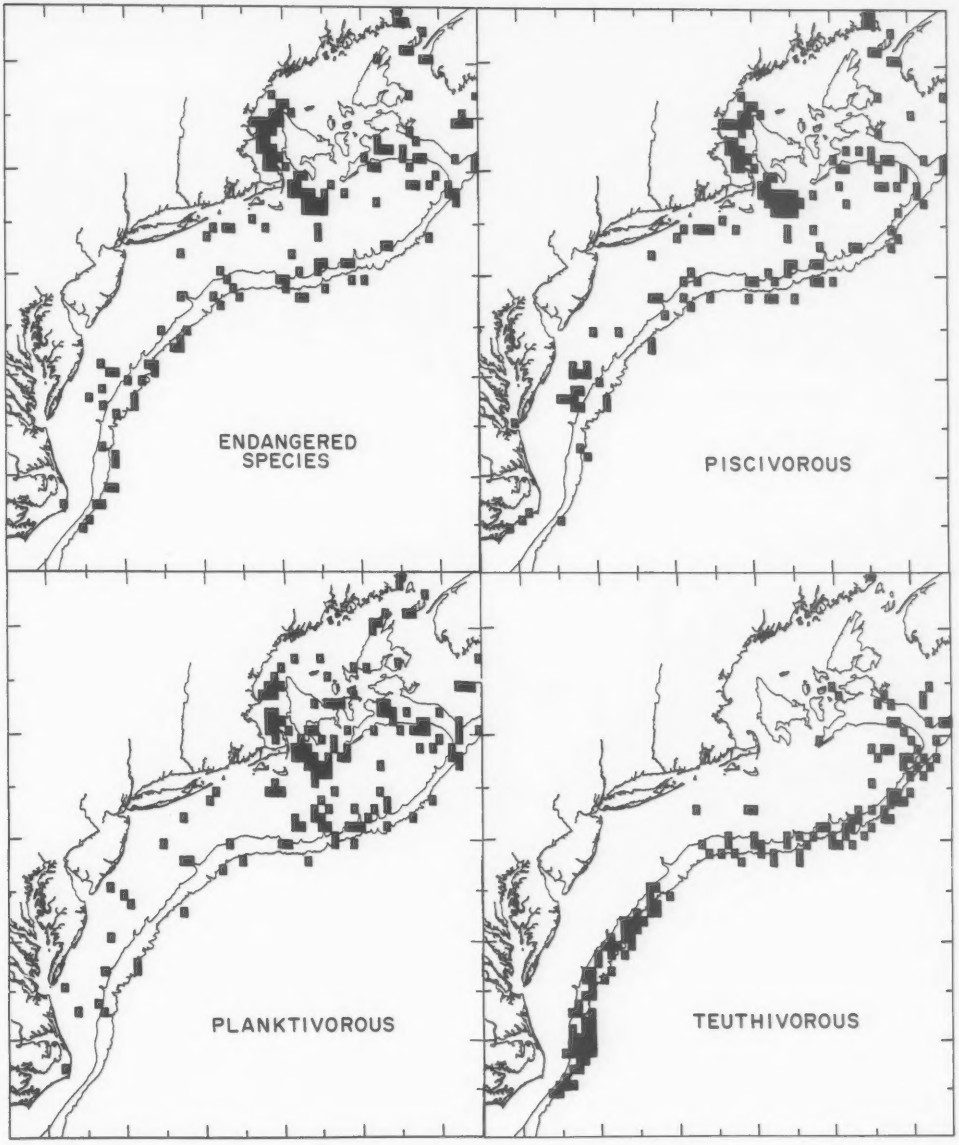

FIGURE 3.—Blocks with top 10% of cetacean biomass per unit effort values for four subsets of the total cetaceans: endangered species (right, humpback, sperm, blue, fin, and sei whales), fish-eating component, plankton-eating component, and squid-eating component.

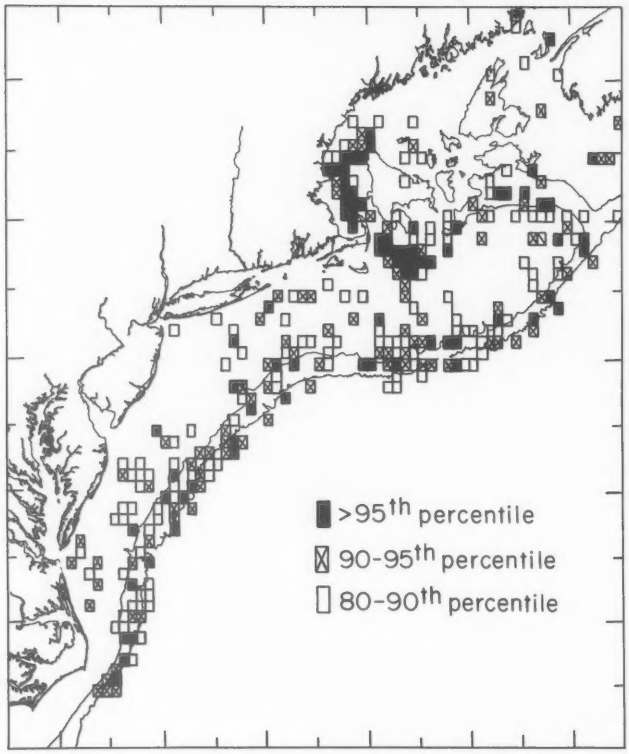

FIGURE 4.—Plot of Habitat Use Index in 10-minute blocks, showing blocks with values in the upper 5%, 10%, and 20% of the distribution.

TABLE 4.—List of the 10-minute blocks with Habitat Use Index values in the upper 1% of all blocks sampled, in descending order, with the latitude and longitude of the block center and the location of the block.

Utilization index	Central point of block		General location
49	42°25′	70°25′	Northern end—Stellwagen Bank
41	41°25′	69°15′	Great South Channel
36	41°25′	69°25′	Great South Channel
34	42°15′	66°25′	Northeast Channel
33	41°35′	69°25′	Great South Channel
32	42°15′	70°25′	Stellwagen Bank
32	42°15′	70°05′	Stellwagen Bank
32	40°35′	67°25′	Georges Banks—Powell Canyon head
29	42°15′	70°15′	Stellwagen Bank
29	42°05′	70°15′	Stellwagen Bank
28	41°25′	69°05′	Great South Channel
27	41°45′	69°45′	Great South Channel
27	41°25′	68°55′	Great South Channel
26	43°15′	69°55′	Northern end—Jeffreys Ledge
26	42°55′	65°35′	Off Browns Bank
26	41°15′	69°15′	Great South Channel

concentrations of high-use blocks tend to be around the perimeter of Georges Bank and along the continental shelf edge.

DISCUSSION

The CETAP sighting data for some individual species showed a concentration of sightings along the western margin of the Gulf of Maine. This analysis has demonstrated quantitatively that this area is the most intensely used cetacean habitat on the northeast U.S. continental shelf. It comprises a major feeding ground for fin whales, humpback whales, right whales, minke whales, and white-sided dolphins. Humpbacks and fin whales are known to feed heavily upon the American sand lance, *Ammodytes americanus*, a small schooling fish (CETAP 1982; Hain et al. 1982; Mayo 1982; Mitchell 1973, 1975c; Overholtz and Nicolas 1979), and the minke whales

and white-sided dolphins likely do so as well (CETAP 1982; Mayo 1982; Mitchell 1975b). The sand lance populations of the western North Atlantic have increased dramatically since the mid-1970's (Sherman et al. 1981). Meyer et al. (1979) described the western Gulf of Maine, especially Stellwagen Bank and east of Cape Cod, as an area of extremely dense sand lance populations. Data from the National Marine Fisheries Service 1979-1981 groundfish surveys (T. R. Azarovitz[5]) also shows peak *Ammodytes* abundance in the Stellwagen Bank-Jeffreys Ledge area. A second area of high sand lance abundance shown by these data corresponds to the midshelf east of the Chesapeake, which was identified above as a region of high use by piscivorous cetaceans. It is likely that sand lance distributions are a primary controlling factor in the pattern of high-intensity habitat use shown here for the western Gulf of Maine.

Ammodytes is not the only cetacean prey species which can be shown to have a strong effect on patterns of cetacean habitat use within the western Gulf of Maine, although it is the major one. The right whale feeds primarily upon copepods (Nemoto 1970; Watkins and Schevill 1976). Right whales are a major component of the cetaceans in the southeasternmost portion of the high-use area in the western Gulf of Maine, in the vicinity of the Great South Channel, where they congregate in response to extremely dense spring concentrations of *Calanus finmarchicus* (CETAP 1982).

The other high-use cetacean habitat we have identified is the edge of the continental shelf. The cetacean assemblage of this region has been analyzed in detail by Hain et al. (1985). The primary species of the shelf edge are sperm whales, pilot whales, gray grampus, saddleback dolphins, bottlenose dolphins, and striped dolphins. Less common species include the various beaked whales and other dolphin species. This assemblage does not specialize on one or two prey species as we have suggested for the Gulf of Maine, but is highly diverse in prey taken, although individual species may exhibit quite narrow dietary specializations. Food items include a wide variety of squids and fishes (Kenney et al. 1985). Furthermore, the shelf edge assemblage on Georges Bank includes sei whales, which feed primarily on copepods and secondarily on euphausiids (Jonsgard and Darling 1977; Mitchell 1975a, 1975b; Nemoto 1970). Sei whales occur primarily on the southwest and eastern portions of Georges Bank. The CETAP data also show sightings of other baleen whales—primarily fin whales, but also minke, humpback, and right whales—near the southern edge of Georges Bank during some times of the year. The shelf edge, although used less intensely than the western Gulf of Maine, supports a cetacean fauna which is much more diverse in terms of both cetacean species and variety of prey taken.

We have interpreted our results in this study as indicating control of cetacean distributions by the distributions of the most important prey species. This is almost certain to be the case on a microscale level, but may or may not be true at the general level. It is unknown how migratory cetaceans orient or navigate to their feeding grounds, but it may be that physical cues from the environment are used in this process, in effect determining or influencing the general pattern of distribution. Another alternative could be that there is a significant traditional or historical component of the return to the same general vicinity each year, with microscale distributions within that region directly related to prey density. In each of these cases the ultimate controlling factor is food, but the proximate factors are something different.

We have limited our discussion of individual species mostly to the descriptive level. One factor, however, should be noted. Because we are dealing with biomass of cetaceans, these patterns are dominated by the large whales for the most part. Because fin whales are easily the most common whale in the region, they are the dominant factor in patterns of cetacean biomass distribution (Kenney et al. 1985; Scott et al. fn. 4). The most common species numerically were white-sided and saddleback dolphins, with estimated populations of each exceeding 30,000 individuals (CETAP 1982), but their contributions to the patterns shown here are smaller because of their relatively smaller sizes. One must refer to the distribution plots in the 1982 CETAP report for the details of individual species distribution patterns.

We have purposely avoided the use of the term "critical habitat" in this analysis. Besides the legal aspects of the term under the Endangered Species Act and Marine Mammal Protection Act, Ray and Miller[6] have pointed out that there are many dimensions to the concept of critical habitat. These include the biological vulnerability of a species, the ecological processes which support the species, and the poten-

[5]T. R. Azarovitz, Northeast Fisheries Center Woods Hole Laboratory, National Marine Fisheries Service, NOAA, Woods Hole, MA 02543, pers. commun. December 1982.

[6]Ray, G. C., and R. V. Miller. 1982. Critical habitats of marine mammals. Paper presented at 1982 annual meeting, International Council for the Exploration of the Seas, ICES C.M. 1982/N:7.

tial impacts of human activities. We have for the most part addressed only the patterns of habitat use, which contribute to the first two dimensions listed above. By giving extra weight to the endangered species in the Habitat Use Index, however, we have also further addressed the dimensions of biological vulnerability and potential impacts. On the other hand, the concept of critical habitat as strictly defined should be limited to single species. We have approached the problem from the viewpoint of the entire cetacean fauna of the region. Our analysis has defined those localities which appear to be important cetacean habitats based on the intensity of utilization with a special emphasis on the endangered species. These results now can and should be used as additional input for resource management and decision-making purposes.

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SOUNDS FROM BRYDE, *BALAENOPTERA EDENI*, AND FINBACK, *B. PHYSALUS*, WHALES IN THE GULF OF CALIFORNIA

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ABSTRACT

Low-frequency moaning sounds were recorded from Bryde whales, *Balaenoptera edeni*, off Loreto, Mexico, in the Gulf of California. These utterances averaged 0.4 s in duration with most of the sound energy at about 124 Hz. Elsewhere in the Gulf, we recorded about 1,300 low-frequency moans from at least 35 feeding finback whales, *B. physalus*. The finbacks' most outstanding sound was a long moan with a 1.9-s component at 68 Hz and a 1.6-s component at 34 Hz. Overall sound source levels in the effective bandwidths ranged between 152 and 174 dB re 1 μPa (1 m) for Bryde whales, and 159 to 183 dB for finback whales. Short "20-Hz signals" that are typically associated with finback whales were not present in these recordings, apparently because of seasonal or behavioral differences.

The main objective of this study was to describe underwater sounds from two species of mysticete whales—the Bryde whale, *Balaenoptera edeni*, and the finback whale, *B. physalus*. We also wanted to compare the presently described finback sounds with those recorded elsewhere.

Contrasted with the typical whistles, squeals, and clicks of odontocetes, we continue to find that mysticetes utter mostly low-frequency sounds. However, exceptional and rare sounds of higher frequency have been reported (Cummings and Thompson 1971; Beamish and Mitchell 1971, 1973; Beamish 1978). The combination of low frequencies (Hz), long wavelengths, and high source levels of mysticete whale sounds enables their detection at distances up to 100 km or more, even with standard signal processing.

Low-frequency sounds (40-75 Hz, 1-s long, and others) have been recorded from finbacks in the North Atlantic (Schevill and Watkins 1962; Edds 1981). Short, powerful "20-Hz signals" have also been recorded from this species (Schevill et al. 1964). Watkins (1981) categorized underwater finback sounds as 20-Hz pulses, ragged broadband low-frequency pulses, low-frequency rumbles, higher frequency sounds, and broadband impulses.

We have long been interested in "20-Hz signals", having worked with many categories from widespread areas of the world (Cummings and Thompson 1966[4]; Northrop et al. 1968, 1971), and the prospects of recording them from the more accessible finbacks in the Gulf of California also was an important objective.

We are unaware of any other descriptions (except for 20-Hz pulses) of sounds from Pacific finbacks. Underwater sounds from the Bryde whale were unknown, this being the original description except for a brief abstract of the present work in 1969 (Thompson and Cummings).

MATERIAL AND METHODS

An expedition took place in June 1969, aboard the 27 m yawl, *Saluda*. The ship left La Paz (southeast Baja peninsula, Mexico) sailed northward to Mulegé, across the Gulf of California to Guaymas on the Mexican mainland, northward past Isla San Esteban, around Isla Angel de la Guarda, and southward to Santa Rosalia—a distance of about 1,500 km (Fig. 1). Except for Contact 3, all of the sounds recorded in the presence of unidentified large whales were generally the same as those that we determined to be from finbacks. However, we were not always certain which balaenopterid was being recorded, especially at long distances. Consequently, if an identification of a balaenopterid whale was questionable, the "contact" was noted simply as "*Balaenoptera* sp".

The water's surface varied from Sea State 0 to 2, and currents usually were minimal. The ship's operating equipment was shut down during all recordings. The instrumentation included a hydrophone-

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[4]Cummings, W. C., and P. O. Thompson. 1966. 20-Hz signals in the northeast Pacific. Unpubl. Rep., 17 p. Navy Electronics Laboratory, San Diego, 92152.

FIGURE 1.—Track of *Saluda* in the Gulf of California (June 1969) with numbered cetacean contacts.

preamplifier (Wilcoxon,[5] Type M-H90-A) suspended at depths of 6 to 53 m below the surface. Up to 800 m of floating cable carried the signals to the ship, allowing the hydrophone to be stationary until the ship drifted out to this distance. The hydrophone was suspended from an inflatable 8 m spar buoy which provided effective acoustic isolation from low-frequency acceleration caused by surface waves. The hydrophone's response was attenuated at low frequencies (beginning with 3 dB down at 12 Hz) to further reduce low-frequency noise and to prevent most of the preamplifier blockage from any drag motion that remained. Without these or similar measures, we have found that hydrophone and sea noise below 100 Hz, even in relatively smooth seas, usually prevents satisfactory recordings of low-frequency mysticete sounds with suspended systems.

One track of a magnetic tape recorder (Magnecord 1020), powered by a DC-AC converter, carried a running commentary and airborne whale sounds from a radio microphone (Vega Telemike). The other track recorded signals from the hydrophone. Continuous visible records were made on station with a level recorder (Brüel & Kjaer, Type 2301), also powered by the converter which was acoustically isolated. A sound analyzer (General Radio, Type 1558) was used to monitor incoming signals and their absolute levels and to provide power to the hydrophone-preamplifier. Calibration was by means of a 1,000-Hz tone and pink or white noise which were inserted through the system and recorded at frequent intervals. Overall response of the recording system was ±5 dB from 25 Hz to 18 kHz.

Without a hydrophone array we could not precisely localize sound sources. However, correlations between whale movements and changes in received sound level provided evidence that those sounds came from the whales observed.

At sea we find it difficult to distinguish the Bryde whale from other balaenopterids, especially the sei whale, *B. borealis*. An exception was the circumstance noted here, involving long contacts and good visibility above and below water, so that identifying features of behavior and form were revealed. Most useful of these field characteristics were 1) the presence of ridges on top of the head of Bryde whales, 2) the asymmetrical coloration of finbacks, usually a yellowish white on the lower right jaw and baleen that is contrasted with the darker appearance of the left area, and 3) the peculiar surfacing of sei whales whereby head and fin appear nearly simultaneously, without arching.

Received overall sound levels are reported in dB re 1 μPa, and source levels are referenced to 1 m. Analysis was accomplished using graphic level recorders, oscilloscopes, a sound spectrographic recorder, and a RTA (real time analyzer).

RESULTS

Sightings and Recordings

The locations of whale sightings associated with recordings of whale sounds are listed (Table 1). Unidentified balaenopterid whales were sighted off La Paz, where two low-level whale sounds were recorded during Contact 1.

We spotted two Bryde whales, about 11 m long, southeast of Loreto (Contact 2). The sea was calm and the surface water temperature was 24°C. The two animals separated as the ship approached. One swam away and remained mostly out of sight. The other began passing back and forth under the ship's keel. It dove about 10 m and surfaced every 1 to 6 min. W. C. Cummings dove on the whale and photographed it underwater for identification.

We recorded 288 low-frequency moans in 50 min from the Bryde whales during Contact 2. Some of these sounds were of very low signal-noise ratio (down into the ambient level of the sea noise) and presumably originated from the more distant of the

[5]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

TABLE 1.—Contacts with sound producing whales in the Gulf of California.

Contact	Date	Time	Location	Subjects (No.)
1	6-11	1000	24°43.5′N, 110°36′W, 2 km S of Isla San Francisco	*Balaenoptera* sp. (1)
2	6-13	0700	25°57.5′N, 110°19′W, 8 km SSE of Loreto	*B. edeni* (2)
3		1930	26°50′N, 111°42′W, 14.8 km SE of Pta. Concepción	*B. edeni* (1)
4	6-17	1815	28°18′N,111°46′W, midway, Guaymas to Isla San Esteban	Large whale (1)
5	6-18	0530	28°25′N, 112°9.5′W, 18.5 km ENE of San Pedro Martir Island	*Balaenoptera* sp. (1)
6		1330	28°58′N, 112°53.5′W, 24.1 km ESE of Isla Angel de la Guarda	*B. physalus* (3)
7	6-19	0900	29°35′N, 113°31′W, 3.7 km ENE of Puerto Refugio	*B. physalus* (about 35)
8		1430	29°41.5′N, 113°27′W, 17.6 km NE of Puerto Refugio	*B. physalus* (2)
9	6-20	1430	29°14′N, 113°33′W, N. end of Ballenas Channel	*Balaenoptera* sp. (1)
10		1530	29°15.5′N, 113°30′W, N. end of Ballenas Channel	*Balaenoptera* sp. (1)

two whales. Coincidently, we were recording low-level, high-pitched whistles and squeals from a distant group of saddleback porpoises, *Delphinus delphis*. It was obvious that changes in the loudness of other low-frequency signals, as aurally monitored, and in the level on the graphic recorder were correlated with the nearby Bryde whale's proximity to the ship.

Later the same day, another whale was sighted off Pta. Concepción in the Mulegé area and tentatively identified as either a sei or Bryde whale of about 12 m (Contact 3). We recorded 407 sounds from this whale. The sounds were essentially the same as those recorded earlier from the Bryde whales of Contact 2. After analyzing the sounds, Contact 3 was identified as a Bryde whale. Sounds of these characteristics were not encountered again during the cruise, nor were any other Bryde whales seen.

About 100 km northwest of Guaymas, a large whale was sighted at a range of about 450 m (Contact 4). A brisk wind and choppy seas prevented identification, but one distinctly whalelike moaning sound appeared in the accompanying noisy recording.

East of San Pedro Martir Island, we recorded 42 sounds from another whale (Contact 5) identified as a finback, about 15 m in length. Three large finback whales were sighted off the southern tip of Isla Angel de la Guarda (Contact 6). All of the 376 moans recorded from these whales occurred when the animals were below the surface.

On 19 June, we sighted about 35 finback whales outside the entrance of Puerto Refugio (Contacts 7, 8). They surfaced in series of 2 to 7 times, usually in pairs or in trios. Their blows were accompanied by smooth resonant sounds similar to that expected from air rushing through a confined space. Climaxing the final appearance in a series of surfacings, the whales strongly arched their backs and appeared to dive at a steep angle. Some of the finbacks' dorsal fins were distorted. Large concentrations of whales, porpoises, and sea lions occurred over an area of at least 6 km around the ship where they

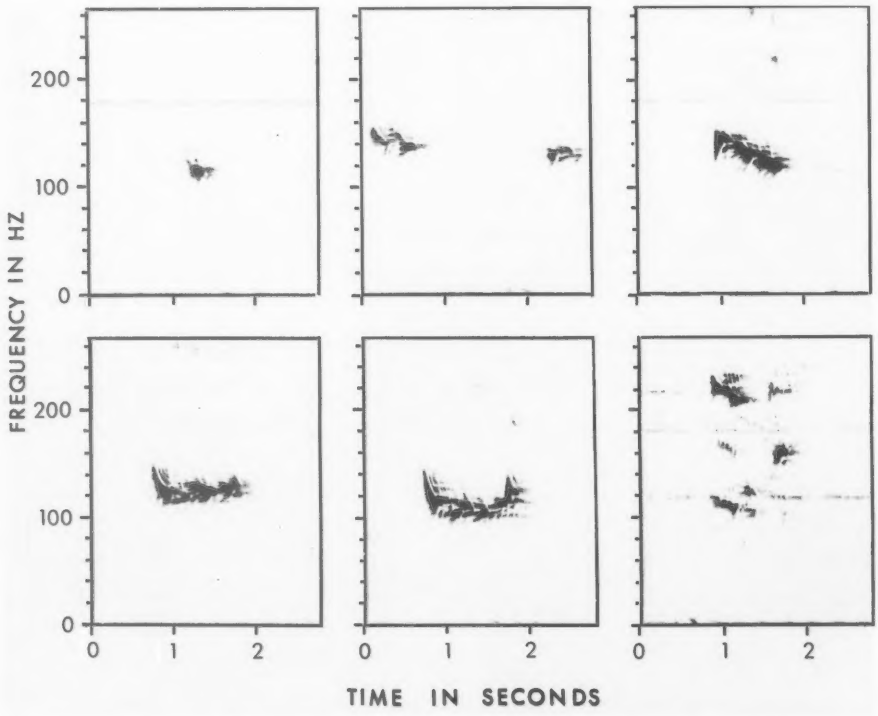

FIGURE 2.—Spectrograms of typical Bryde whale moans. The effective analyzing filter bandwidth was 3 Hz.

were feeding on red crabs, *Pleuroncodes planipes*, that swarmed at the surface during the early morning and evening. We distantly accompanied two of the whales which were swimming at 18 km/h and surfacing every 1 to 1.5 min. They rose high enough above the surface for us to clearly identify them as finbacks. Extensive sound recordings were made among the large concentration of whales near shore (Contact 7) and also much farther offshore (Contact 8), away from the main group.

Recordings of whale sounds from Contacts 9 and 10 were made in Ballenas Channel near finned whales on the west side of Isla Angel de la Guarda.

Analysis of Whales Sounds

Most sounds attributed to Bryde and finback whales, other than those from blows, were in a class we called "moan"—emissions longer than 0.2 s and <250 Hz in frequency. Many other sounds of biological origin, including clicks, knocks, etc., were recorded in the presence of the whales, but only when other possible sources were present, such as porpoises and sea lions.

Bryde Whales

As seen in Figures 2 and 3, upper, Bryde whale

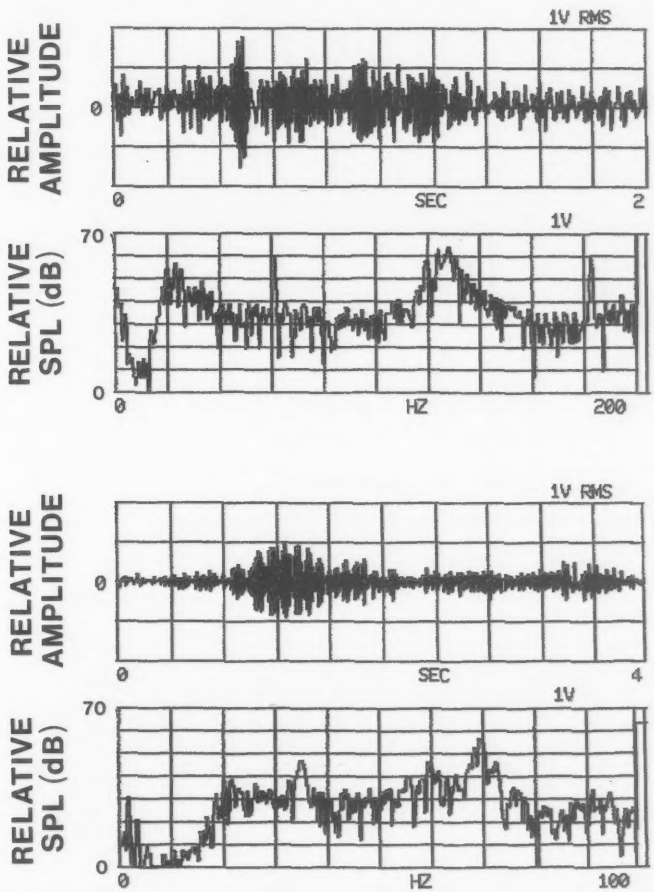

FIGURE 3.—Waveform and spectrum (/Hz) for Bryde whale (upper) and finback whale (lower). Effective analyzing filter bandwidth was 0.75 Hz (Bryde whale sound), 0.375 Hz (finback whale).

moans varied widely in duration and frequency (Hz). Of the 93 miscellaneous moans analyzed (Table 2), the principal sound energy occurred at a mean frequency of 124 Hz; that of individual moans varied from 70 to 245 Hz. Seventy-three percent of these sounds exhibited frequency shifts (mean of 15.2 Hz) that were downward or upward, or a combination thereof. The mean duration of the moans was 0.42 s (range, 0.2 to 1.5). These sounds occurred at intervals of 0.2 to 9 min.

The Bryde whale that apparently was attracted to the ship (Contact 2) did not emit moans when very closeby. The received overall sound level for a typical moan, when this whale was estimated to be 300 m away, was 102 dB. Assuming a spherical spreading loss of 20 $\log_{10}$ 1.094(R), R being distance in

TABLE 2.—Analysis of whale sounds.

		68/34-Hz moans				Miscellaneous moans					
Contact	Identification	No.[1]	Range (m)	Received level (dB)[2]	Source level (dB)[3]	No.[1]	Mean frequency (Hz)	Duration (s)	Range (m)	Received level (dB)[2]	Source level (dB)[3]
1	*Balaenoptera* sp.	2(2)	—	83	—	0	—	—	—	—	—
2	*B. edeni*	0	—	—	—	288(93)	123.9	0.42	300	102	152
3	*B. edeni*	0	—	—	—	407(35)	132.0	0.40	600	116	168
									250	126	174
4	Large whale	0	—	—	—	1(1)	75.0	0.60	—	90	—
5	*Balaenoptera* sp.	30(10)	250	121	169	12(8)	49.6	0.55	200	121	166
	No visual contact	44(16)	—	90	—	21(21)	50.7	0.63	—	92	—
6	*Balaenoptera* sp.	203(6)	2,000	115	183	173(14)	53.7	1.23	2,000	115	183
7	*B. physalus*	164(20)	—	108	—	468(131)	59.8	0.59	100	125	165
8	*B. physalus*	201(30)	—	99	—	550(42)	65.5	0.73	—	117	—
9	*Balaenoptera* sp.	3(3)	2,000	95	—	102(17)	63.3	0.70	2,000	118	181
10	*Balaenoptera* sp.	90(5)	800	108	166	12(8)	77.5	0.68	800	101	159

[1]Number of sounds encountered with number analyzed in parenthesis. [2]dB re 1 μPa. [3]dB re 1 μPa at 1 m.

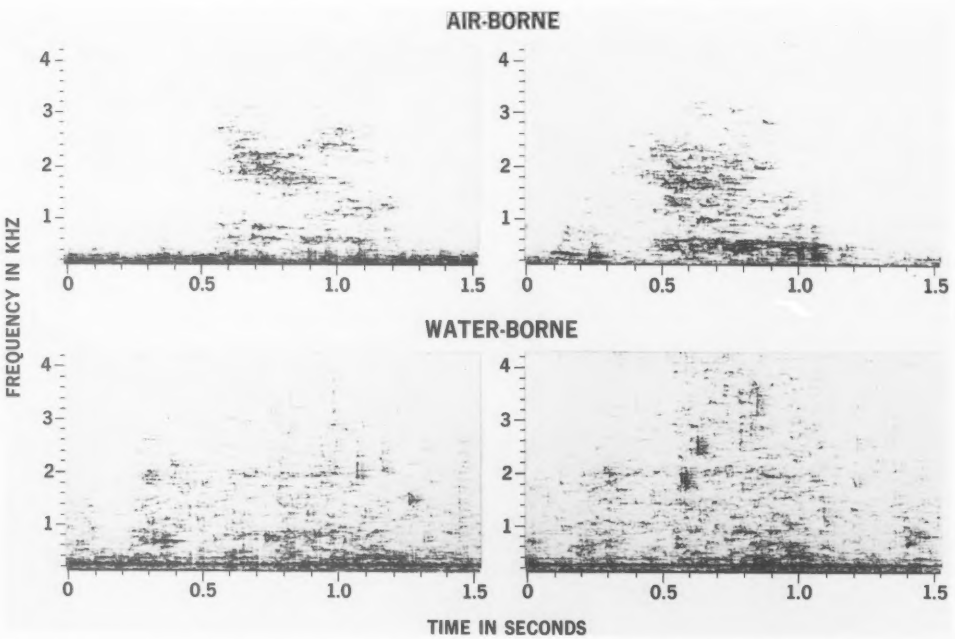

FIGURE 4.—Spectrograms of two blows from a Bryde whale recorded in air (upper) and in water (lower). The effective analyzing filter bandwidth was 20 Hz.

meters, this received level would indicate an overall source level of 152 dB in the effective bandwidth. The whales were close enough and the frequencies low enough that attenuation was probably minimal. However, these particular moans could possibly have been emitted by the other whale that was about 500 m away at the time. In this case, the estimated overall source level would have been 157 dB in the effective bandwidth.

Weak exhalation sounds were recorded simultaneously from underwater and in the air from the nearby surfaced Bryde whale. The exhalation sounds received underwater were nearly obscured by splashing sounds as the animal broke the surface (Fig. 4).

For the 35 moans analyzed from the Bryde whale of Contact 3, the mean frequency of the strongest component was 132 Hz and the mean duration was 0.40 s, both values close to those from Contact 2 (Table 2). However, the overall source level estimates of 168 and 174 dB (in the effective bandwidths) were greater.

The nearby Bryde whale (Contact 2) was totally submerged as it produced all of its moaning sounds, but no other apparent behavior was associated with the moans.

Finback Whales

In addition to miscellaneous moans (Fig. 5) that were similar to, but lower in frequency than those recorded from Bryde whales, the sounds of identified finback whales (Contacts 7, 8) included unique moans characterized by a long 68-Hz component that was usually followed by another component at 34 Hz (Figs. 6, 3 (lower)). Of the miscellaneous moans analyzed from recordings of the finback whales of Contacts 7 and 8, the mean frequency of the strongest component was 59.8 and 65.5 Hz, and the mean duration was 0.59 and 0.73 s, respectively (Table 2). Typically, these moans showed some frequency shift with <10% of the signals changing more than 20 Hz, generally downward. Overall source level

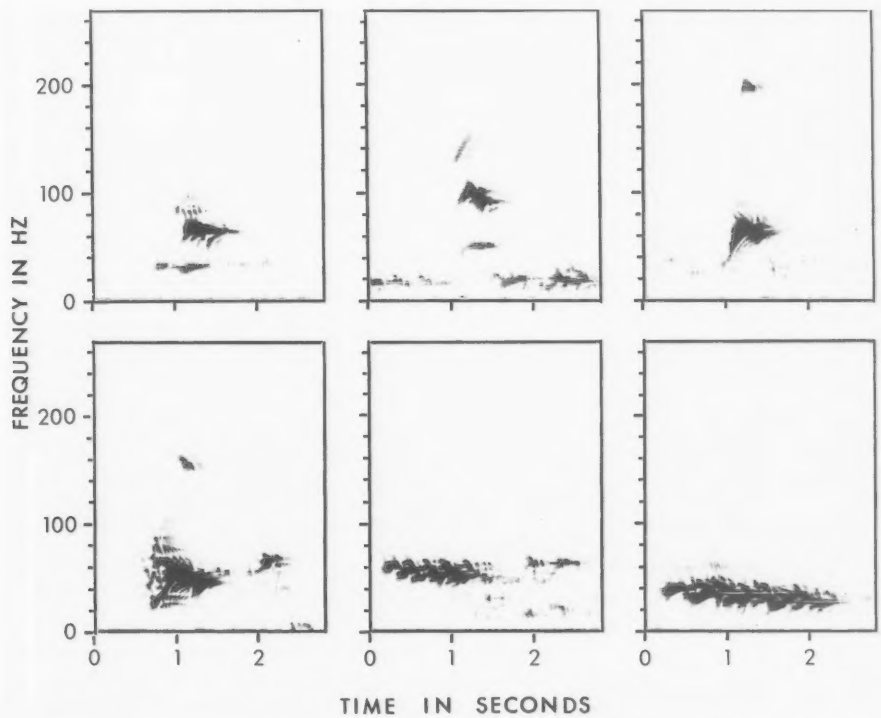

FIGURE 5.—Spectrograms of miscellaneous whale moans from finback whales off Isla Angel de la Guarda. The effective analyzing filter bandwidth was 3 Hz.

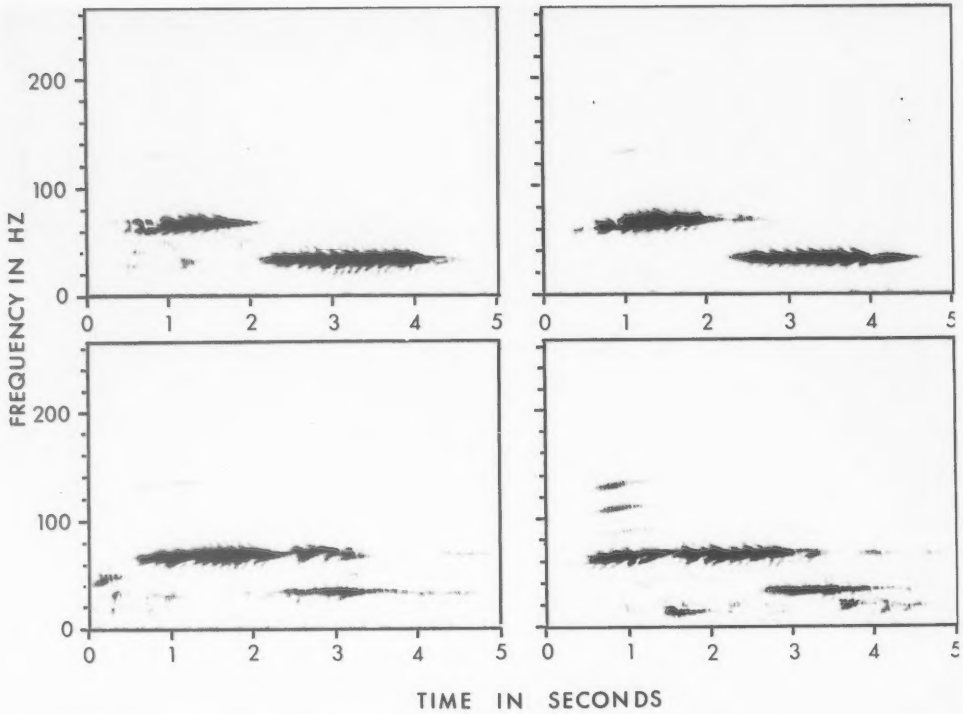

FIGURE 6.—Spectrograms of typical 68/34-Hz moans from finback whales recorded off Isla Angel de la Guarda. The first component of the moans began at 65 Hz and increased to 68 Hz in the first sec. It was accompanied by weaker modulation products at about 23-Hz intervals, mostly above the main frequency. The 34-Hz component followed and sometimes overlapped the first component (lower spectrogram). The effective analyzing filter bandwidth was 3 Hz.

of the sounds was 165 dB in the effective bandwidths.

Of the 50 long moans from finbacks that were analyzed, the mean frequency of the main, or first, component was 68.2 Hz; the mean frequency at onset being 66.1 Hz. The mean duration was 1.5 s. Thirty moans exhibited additional lower frequency components with a mean frequency of 33.5 Hz and a mean duration of 1.3 s. The overall mean duration of these two-part moans was 3.1 s. The 365 moans of this type encountered in Contacts 7 and 8 occurred on the average of 1.6 and 2.2 times/min, respectively.

In the case of unidentified balaenopterid whales, the mean frequency of the strongest component of the 68 miscellaneous moans analyzed was 58.5 Hz (range from 15 to 95 Hz), and the mean duration was 0.8 s. Of these sounds <10% had any frequency shift >10 Hz. Thirty-seven of the analyzed moans were the same as the long two-part moans recorded in the presence of finbacks. Their mean frequencies were 68.1 and 34 Hz, the mean component duration was 1.9 and 2.6 s, respectively, and the mean total duration was 3.4 s. The mean starting frequency of the 68-Hz component was 63.9 Hz. These two-part moans occurred at a rate of 1.5 to 3.2/min. Overall source levels ranged from 159 to 183 dB in the effective frequency bandwidth.

The blows of finback whales were as high as about 7 m above the water's surface, and often they were clearly audible in air at distances out to 200 m. The last blow in a series was followed by an inhalation that sometimes involved a low-frequency whistlelike sound just before a long dive (Fig. 7). The physical characteristics of blow sounds varied slightly from one whale to another, providing a certain degree of uniqueness for an individual whale (Fig. 7). Wheezing, shriek, and hornlike sounds produced by humpback whales in association with their blows have been described by Watkins (1967) and Thompson et al. (1977).

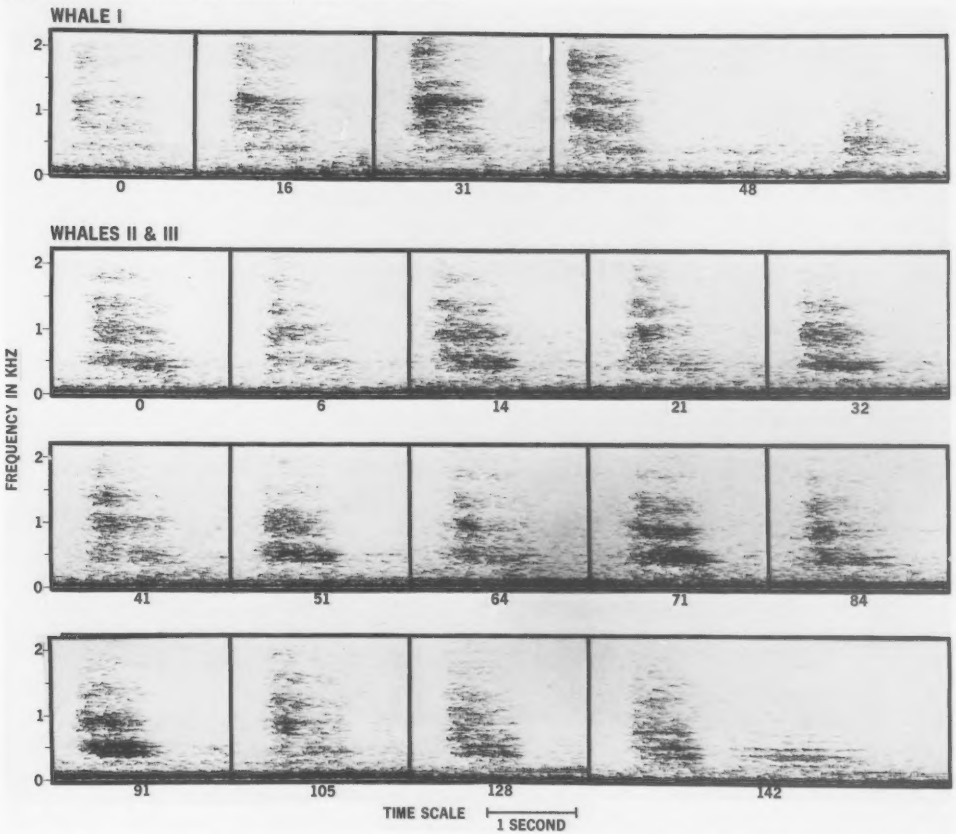

FIGURE 7.—Spectrograms of whale blow series recorded in air. Running time in seconds relative to the first blow is indicated on the abscissa. Whales II and III (second series) can be distinguished throughout the first 105 min by the unique physical characteristics of their alternating blows. Just before a long dive, the whales produced a low-frequency whistlelike sound at inhalation (last spectrogram, first row; last spectrogram, last row) which was not apparent during earlier blows of a series. In the second series, two low-level blow sounds at 110 and 132 min are not shown. The effective analyzing filter bandwidth was 20 Hz.

DISCUSSION

The moans recorded on this cruise from visually unidentified or unseen whales were very similar to those found to be from finbacks, except for Contact 3 involving Bryde whale sounds. Thus we believe the former also were from finback whales.

Some of the moans recorded in this study only slightly resembled short "20-Hz signals" described by several investigators (Walker 1963; Patterson and Hamilton 1964; Schevill et al. 1964; Weston and Black 1965; Cummings and Thompson 1966 [fn. 4]; Northrop et al. 1968; Watkins 1981). However, none of the presently described signals could be categorized as short "20-Hz signals" noted in other studies, because of differences in frequency (Hz) of major sound energy, signal repetition, and intervals between repetitions. Typical short "20-Hz signals" are narrowband pulses with principal sound energy near 20 Hz. They are repeated at remarkably constant intervals. Only about 3% of the sounds reported here had components as low as 20 Hz.

The miscellaneous moans that were recorded from finbacks mainly resemble the category that Watkins (1981) called "higher frequency sounds". However, most of his recordings of these sounds were downward-sweeping pulses, e.g., 75-40 Hz, with emphasis around 40 Hz. We did not record sounds similar to Watkins' low-frequency rumble or ragged pulse

categories, nor did we record his nonvocal, sharp impulsive category.

Our experience with finback and Bryde whales in the Gulf of California showed that underwater-generated sounds were not produced when visible animals were at or very close to the surface. Exceptions were those sounds which, although principally airborne (e.g., blow and snort sounds), established a physical coupling with the water medium allowing detection by hydrophone. The typical short "20-Hz signals" noted from finback whales in other locations (Northrop et al. 1968) appear in trains that are interrupted after 3 to 22 min of pulsing (equivalent to expected dive times, Fig. 8). We believe that these interruptions that last from 1 to 6 min represented surface time. Blue whale sounds in southeast Pacific waters had silent interruptions that were associated with surfacing and ventilation (Cummings and Thompson 1971). Winn et al. (1970) correlated certain "cries" and "ratchet" sounds with surfacing behavior of humpback whales. Data from the present cruise, our recordings of typical short "20-Hz signals", our recordings from blue whales, and from work on humpback whales, apparently reveal surface and dive times as learned through monitoring underwater whale sounds.

Possible explanations for our lack of 20-Hz short pulses in the presently described recordings and for the absence of other classes of sounds that Watkins (1981) has commonly recorded from finbacks are seasonality and insufficient sampling. We now know that seasonality is involved.

Watkins (1981) recorded the pulses in the North Atlantic only from late October to early May. Cummings and Thompson (fn. 4) recorded them in the North Pacific from September to April, and Thomp-

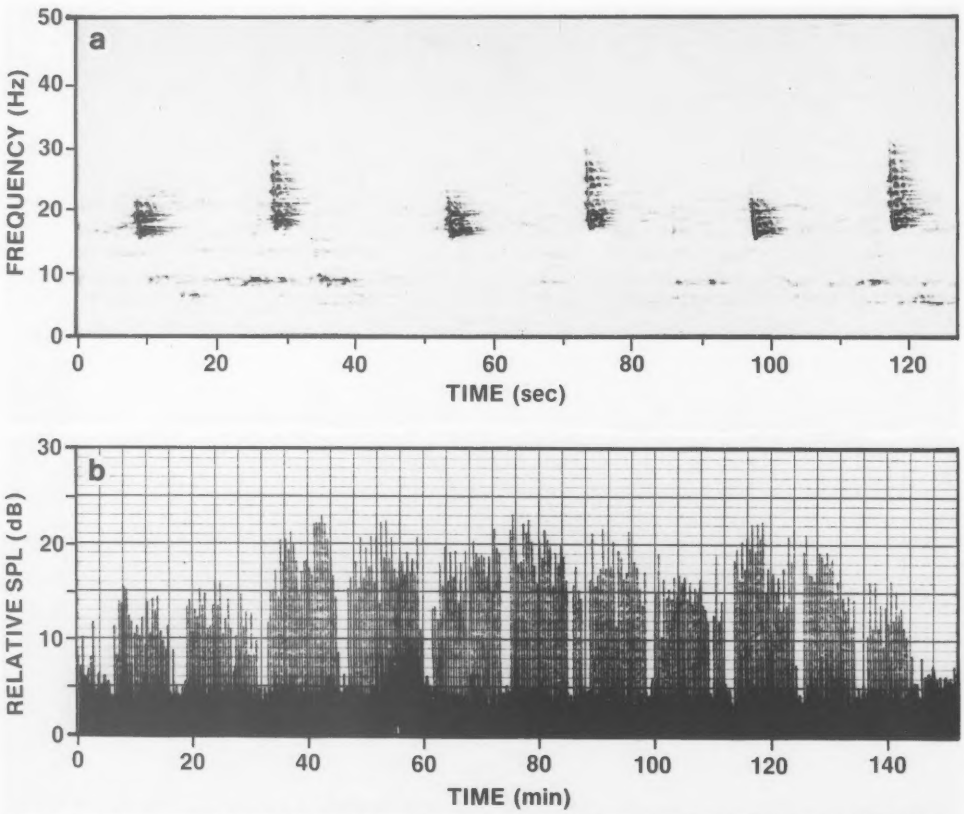

FIGURE 8.—(a) Spectrogram of short "20-Hz signals" from finback whales; the effective analyzing filter bandwidth was 0.4 Hz. (b) Strip chart showing 11 trains of short "20-Hz signals" with interruptions between; the filter passband was 12.5-25 Hz.

son and Friedl (1982), working off Hawaii, recorded them only from the end of August to late April. Northrop et al. (1968), in the North Pacific, noted them from October to March. Finally, in recordings from finbacks in March 1985 (Gulf of California) typical 20-Hz short pulses were the predominant sound (Thompson et al.[6]). Like the well-known songs of humpback whales, these sounds are probably a manifestation of social or other behavior which occurs seasonally. According to Watkins (1981) they "perhaps were a courtship or reproductive display". Watkins and others apparently have not noted our frequently recorded 68-34 Hz long moans.

There have been many technical advances in bioacoustic signal acquisition and processing. Long-term recordings can be used for obtaining information about certain behaviors, presence or absence of animals, or perhaps distribution of a given species, without the presence of an observer (Cummings et al. 1983). Great gains are being made in the field of signal processing wherein computer- and optically aided automatic acoustic pattern recognition is possible for a number of sounds with recognizable physical criteria. However, regardless of technical advances, the use of such tools is severely limited without first knowing the behavioral significance of the animal sound production. In reality, the two are mutually dependent. An analogous situation would be the use of the most refined instrumentation available for listening in on a conversation carried out in a foreign language that is unfamiliar to the observer. Although extremely difficult to fulfill, the need for related behavioral information on finback whales is paramount.

For these and other reasons, descriptions of sounds from identified sources should be given in detail along with adequate description of the recording instruments. Recording procedures and analyses can greatly affect the apparent variability of sounds. Moreover, one must be careful to consider the large variety of sounds that is apparent in any species of marine mammal (including the finback whale, as shown in this report) and the relatively limited number of recorded sounds of any species.

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INCREASED FOOD AND ENERGY CONSUMPTION OF LACTATING NORTHERN FUR SEALS, *CALLORHINUS URSINUS*

MICHAEL A. PEREZ AND ELIZABETH E. MOONEY[1]

ABSTRACT

Data from pelagic northern fur seals, *Callorhinus ursinus*, taken during 1958-74 by the United States and Canada in the eastern Bering Sea were analyzed to determine relative feeding rates of lactating and nonlactating females. Estimates of the quantity of food and energy consumed by these seals during July-September were evaluated. The average daily feeding rate (adjusted for percentage of time feeding at sea) for lactating seals is 1.6 times that for nonlactating seals. During July-September, the total population of lactating and nonlactating females were estimated to consume 146.5×10^3 t (204.5×10^9 kcal) and 43.1×10^3 t (60.2×10^9 kcal) of food respectively. Fish accounted for 66.4% of food biomass (69.4% of total energy consumption); squid, the remainder.

The energetics of reproduction, especially during lactation, are poorly documented for free-ranging animals. The various reproductive states of domestic mammals, e.g., cattle, sheep, etc., have been extensively studied; and there has also been considerable research on rodents, e.g., mice, voles, etc., under both laboratory and field conditions. As a result of these studies it is widely accepted that most nursing females require considerably more energy than do nonnursing females of the same species, age, and size. Brody (1945) also noted that the maintenance requirements of lactating animals are elevated relative to nonlactating animals.

In some mammalian species, food intake during lactation may be up to 5 times greater than that observed in nonpregnant, nonlactating adult females, and lactating animals often convert considerable body substance to support the lactation process (Baldwin 1978). Previous studies on terrestrial mammals have specifically shown increased energy consumption by lactating females relative to nonlactating females. For example, captive deer mice, *Peromyscus maniculatus*, have a 96% to a 194% increase (Stebbins 1977); and ewes have a 116% increase (Engels and Malan 1979). The bat, *Myotis thysanodes*, which undergoes thermoregulatory physiological changes during reproductive stages, also has higher energy requirements for lactating females (Studier et al. 1973). Lactating humans are recommended to increase food consumption by at least 25% (Eagles and Randall 1980); however, some lactating humans in Guatemala meet their additional lactation energy costs by fat loss (Schutz et al. 1980).

There are few studies on the energetics and consumption of food during lactation by marine mammals. Lactation appears to drain the energy reserves of large baleen whales; the blubber of lactating females (e.g., blue, *Balaenoptera musculus*, and fin, *Balaenoptera physalus*, whales) is lean and emaciated compared with nonlactating females (Lockyer 1978, 1981a). Lockyer (1981b) estimated that adult female sperm whales, *Physeter macrocephalus*, need to increase their food intake by about 32-63% during lactation, meaning that they would need to feed 4 or 5 times daily to meet higher energy requirements. Lockyer (1981b) also estimated that minke, *Balaenoptera acutorostrata*, and fin whales increase their food intake by 75 and 86%, respectively. Spotte and Babus (1980) did not find a significantly increased mean feeding rate for one captive, pregnant bottlenosed dolphin, *Tursiops truncatus*, but standard deviations were consistently greater. In addition, during the first 3½ mo of lactation, a captive mother bottlenosed dolphin consumed 170% more food than she did while not lactating the following year (Mooney[2]). Costa and Gentry (in press) derived metabolic rates for lactating female northern fur seals from measurements of water flux and discussed the components of the

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energy budget for females and pups during the first two months of the reproductive cycle.

Although most mammals ingest more food while they are lactating than they would in a nonlactating state, many species of phocid seals fast during the lactation period (Harrison 1969). These seals (e.g., gray seal, *Halichoerus grypus*, and northern elephant seal, *Mirounga angustirostris*) do not feed from parturition to weaning of the young, and all of their energy needs during lactation must be met by metabolism of in situ energy such as fat reserves. This behavior has been well documented for the gray seal (e.g., Amoroso and Matthews 1951, 1952; Fedak and Anderson 1982) and also for the harp seal, *Phoca groenlandica*, (Lavigne et al. 1982). However, metabolism of fat reserves does not reduce the energetic costs of producing offspring; it merely shifts the time that energy must be acquired, at some energy cost for storage (Millar 1978).

The objectives of this study were to show, using both stomach content and body mass data, that lactating female fur seals ingest more food than nonlactating females in order to meet their increased energy requirements for maintenance and milk production, and to make estimates of the magnitude of this difference in food ingestion. For this study, we utilized data from postpartum and nonpregnant adult, female northern fur seals, *Callorhinus ursinus*, taken pelagically during 1958-74.

METHODS

Data on the contents of stomachs from the female northern fur seals taken pelagically (Fig. 1) in the eastern Bering Sea during 1958-74 by the United States and Canada were analyzed to determine the relation between lactation and food consumption during the summer breeding season. Only data from female fur seals (age $\geq$4 yr) which had information on both body mass and stomach content mass were included. Age was determined from longitudinal half-sections of the upper canine teeth by counting the annual growth layers in the dentine, a method widely accepted by researchers during recent decades to determine the age of many species of mammals (Klevezal' and Kleinenberg 1967). Methods used during 1958-74 to determine age, reproductive status, and the different items in the stomachs were discussed by Lander (1980).

The data used in this study represented stomach contents under different stages of digestion; however, it was not possible to make comparisons between stages because no data on stages of digestion were recorded. Rates of digestion of all prey were assumed to be similar for all females during the same time interval. In our study, all postpartum females were considered lactating, and all nonpregnant (not postpartum) females were considered nonlactating.

Statistical Methods

The cumulative frequency distributions of data on mass of total stomach contents for both lactating and nonlactating females were compared using the one-tail Kolmogorov-Smirnov two-sample test (Siegel 1956).

Data from seals with empty stomachs or stomachs with only a trace of contents (i.e., <10 cc) were considered as zero mass and pooled with data from seals with food in their stomachs. Data for different ages and months were pooled to provide sufficient sample size for analysis because the normal approximation to compute confidence limits is only valid if sample sizes are adequate (Cochran 1977). In order to use parametric statistics, and yet not seriously violate basic assumptions of normality, data were transformed by the modified arcsine transformation discussed by Zar (1974):

$$X = \sqrt{M + 0.5} \quad \arcsin \quad \sqrt{(S + 0.375)/(M + 0.75)}$$

where M is the net body mass (excluding mass of stomach contents, S) and X is the transformed value. This equation was used because of its utility where a large number of the data were from stomachs containing only a trace or less.

The transformed values on the mass of total stomach contents (expressed as a percentage of net body mass) obtained from the above equation were transformed back to percentages to obtain means. We calculated an index of the relative intake of food by lactating females compared with that of nonlactating females by multiplying the ratio of their respective mean mass of stomach contents by 100. The t-test for two independent samples, with the assumption of unequal variance (Snedecor and Cochran 1980), was used on the transformed data to determine if any significant difference in total food consumption and body mass existed between females of different reproductive status.

The relative importance of individual prey in the total diet was assessed using the modified volume percentage method (Bigg and Perez 1985). Only foods with fleshy remains were used as evidence of diet in this method, and the procedure combined the traditional methods of volume and frequency of occurrence. The proportion of total fish and total squid

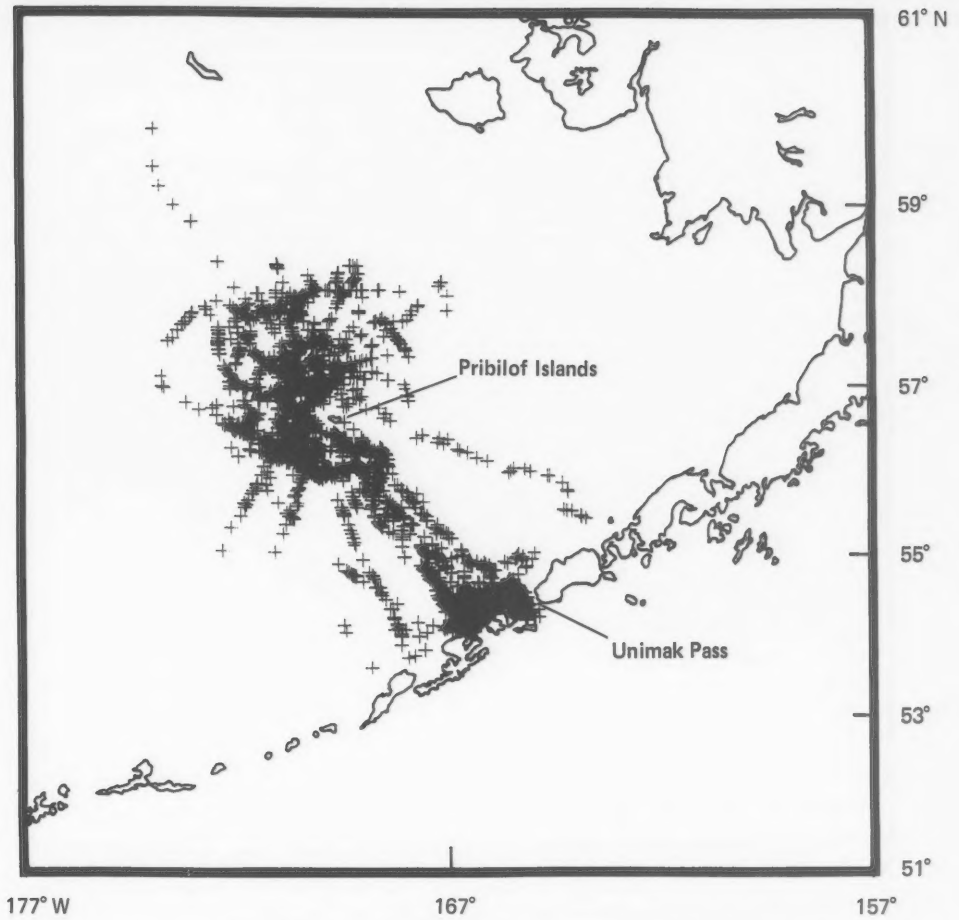

FIGURE 1.—Locations where 3,494 adult female northern fur seals (ages ≥4 yr), whose data were analyzed in this study, were taken by the United States and Canada in the eastern Bering Sea during July-September 1958-74.

in the diet was determined by frequency, while the ration of each species within only fish and squid was determined by volume. Statistical comparison of the diets of lactating and nonlactating females included 1) the Spearman rank correlation coefficient (Siegel 1956; Fritz 1974), 2) percentage similarity (Goodall 1973), and 3) 2 × 2 contingency table analysis (Zar 1974) on the number of stomachs with fish or squid.

Feeding Time at Sea

The largest breeding population of northern fur seals (currently estimated at 8.7×10^5 for a declining population; North Pacific Fur Seal Commission 1984) resides on the Pribilof Islands during the summer months. Pups first appear in late June (Bartholomew and Hoel 1953) and the mean date of pup birth based on recent data is 5 July (Gentry and Holt in press); a date median between values cited by Bartholomew and Hoel (1953) and Peterson (1968). After this time, adult females spend a number of days on shore in several visits to the islands during June-November, and the intervening days between these visits at sea foraging for food (Bartholomew and Hoel 1953; Peterson 1968). They do not feed daily.

Once arriving at the rookery, a parturient female gives birth to one pup, initiates lactation, comes into estrus, and copulates with a male, but does not feed. Gentry and Holt (in press) provided data showing that the average adult female is on shore about 1 d before and 7.4 d after parturition. Each subsequent shore visit lasts about 2.2 d (Peterson 1968; Gentry and Holt in press). The duration of the first sea trip is the shortest (4.8 d), with the duration of the subsequent sea trips increasing at a rate of an additional 1.2 d/30 d postpartum (Gentry and Holt in press).

Recent data collected on the Pribilof Islands by Gentry and Holt (in press) suggests that nonpregnant (= nonlactating) adult females arrive later (about 8 d) on the rookeries and that they may show a somewhat different behavioral pattern than pregnant females. Their first foraging trip at sea is longer (8.9 d), but each of their subsequent shore visits is of constant duration (2.5 d). From these data we derived values for total percent of time spent at sea during July-September (92 d) for the average adult female. Assuming birth of pups on 5 July, this was 69.3 and 75.9% for lactating and nonlactating females, respectively. However, it should be noted that individual females vary from these averages because the period during which adult females first arrive on the rookeries extends over 30 d (Bartholomew and Hoel 1953; Peterson 1968; Gentry and Holt in press).

Feeding Rate Calculations

Bigg et al. (1978) provided data on feeding rates for three captive adult female northern fur seals. Their data for these seals were 5,977 kcal/d (3.0 kg; 6.7% of body mass), 6,118 kcal/d (3.1 kg; 7.6% of body mass), and 5,055 kcal/d (2.5 kg; 8.5% of body mass). These captive northern fur seals were maintained with a diet of Pacific herring (2.01 kcal/g during winter), and it was necessary to consider the energetic concentration of the seal's diet in the wild with respect to the data in Bigg et al. (1978). We derived the following relationship from these data:

$$\text{Daily energy consumption (kcal/d)} = 375.47\ M^{0.75}$$

by averaging the results given for the three captive seals. We calculated average daily feeding rates using this relationship and data on seal body mass.

RESULTS

Body Mass

Table 1 gives the mean values of body mass of adult female northern fur seals (age ≥4 yr) taken during June-September in the eastern Bering Sea and western Alaska. During July-September, the average lactating female (mean 35.3 kg, median age 10 yr) had a body mass 1.13 times that of the average adult nonlactating female (mean 31.1 kg, median age 5 yr; seals age ≥4 yr only). However, as Figure 2 shows, lactating and nonlactating females of the same age were similar in body mass. The differences shown in Table 1 are primarily due to the higher proportions of lactating females at older ages (Lander 1981).

Lactating females exhibited a significant ($P < 0.001$) loss of 7.1 kg of body mass between June and July following parturition (Table 1). This is based

TABLE 1.—Body mass (minus stomach contents mass) of lactating (postpartum) and nonlactating female northern fur seals (ages ≥4 yr pooled) taken pelagically in the eastern Bering Sea and western Alaska, 1958-74.

	Lactating		Nonlactating	
Month	n	$\bar{x}$ and 95% C.I. (kg)	n	$\bar{x}$ and 95% C.I. (kg)
June	[1]499	41.10 ± 0.54	128	29.77 ± 1.41
July	743	34.04 ± 0.42	376	31.49 ± 0.70
Aug.	1,481	35.62 ± 0.30	551	31.05 ± 0.57
Sept.	305	36.46 ± 0.34	118	30.19 ± 1.36
July-Sept.	2,529	35.26 ± 0.23	1,045	31.11 ± 0.42

[1]Pregnant (prepartum) females. Body mass does not include fetal mass.

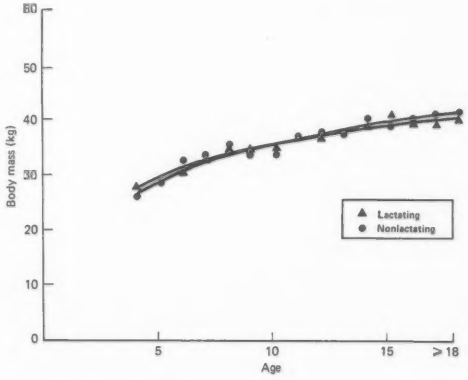

FIGURE 2.—Mean body mass (minus stomach contents mass) of lactating and nonlactating female northern fur seals by age taken pelagically in the eastern Bering Sea and western Alaska during July-September 1958-74.

on data for pregnant females, after excluding fetal mass, which we used to represent body mass of lactating females prior to parturition. Figure 3 shows that this loss in body mass occurred for all ages.

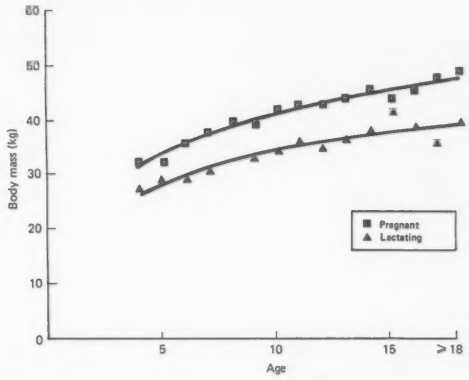

FIGURE 3.—Mean body mass (minus stomach contents and fetal mass) of pregnant (prepartum) and lactating (postpartum) female northern fur seals by age taken pelagically in the eastern Bering Sea and western Alaska during June and July respectively (1958-74).

Relative Food Intake

We found a significant difference ($P < 0.05$) in the relative magnitude of food consumption between lactating and nonlactating female northern fur seals during July-September, but not October, and Figure 4 shows the relative percentage frequency of the number of lactating and nonlactating adult females showing different masses of stomach contents during July-September (pooled data). It is apparent that a greater proportion of lactating females contained food in their stomachs. Lactating females significantly ($P < 0.001$) ingested more food because they had lower cumulative percentages of empty stomachs and stomachs with smaller quantities of food than did nonlactating females.

Table 2 presents the results of analyses between lactating and nonlactating females for the July-September period by time of collection during the day. Our calculated values of the index of relative food intake after sunrise were 162% during 0-3 h, 166% during 4-7 h, 537% during 8-11 h, and 585% during 12-15 h ($P < 0.05$). The calculated index values during 8-15 h after sunrise are excessive, presumably an artifact of food digestion in the stomach.

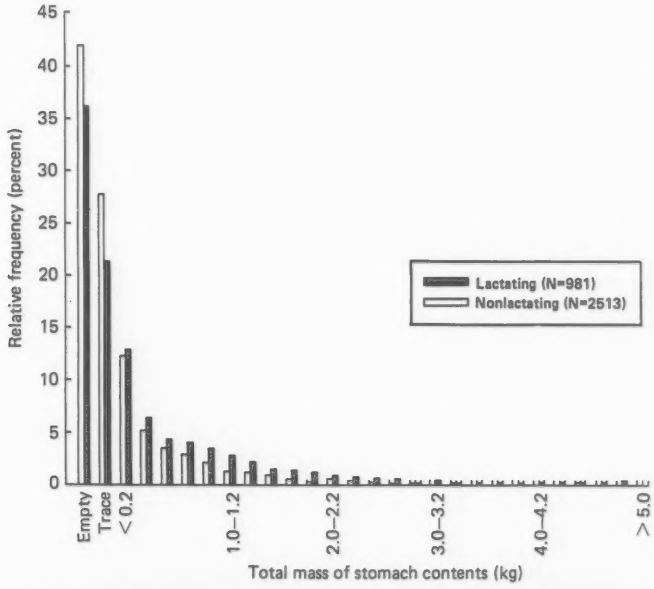

FIGURE 4.—The relative percentage frequency of lactating and nonlactating female northern fur seals (age ≥4 yr) by total mass of stomach contents during July-September.

TABLE 2.—Body mass and arcsine transformed mass of stomach contents (expressed as a percentage of body mass) for lactating (LACT) and nonlactating (NON) female northern fur seals (age ≥4 yr) by hour of collection after sunrise during July-September 1958-74. The relative consumption index (percentage expression of the ratio of the proportion of body mass which was stomach contents for lactating females relative to that for nonlactating females) is also given.

Hours after sunrise	Reproductive condition	n	Body mass (kg) $\bar{x}$ and 95% C.I.	Mass of stomach contents as percentage of body mass: Arcsine units $\bar{x}$	Arcsine units SE	Percentage units $\bar{x}$	Relative consumption index (%)	P[1]
0-3	LACT	312	35.7 ± 0.7	1,355.81	57.24	1.558	161.6	<0.05
	NON	108	31.4 ± 1.5	997.74	83.33	0.964		
4-7	LACT	1,070	35.5 ± 0.4	623.22	25.86	0.333	165.7	<0.05
	NON	381	31.1 ± 0.7	453.29	35.42	0.201		
8-11	LACT	906	35.0 ± 0.4	408.80	24.46	0.145	537.0	<0.05
	NON	365	31.4 ± 0.7	167.27	20.22	0.027		
12-15	LACT	225	34.6 ± 0.7	415.60	47.64	0.152	584.6	<0.05
	NON	127	30.5 ± 1.2	161.66	36.38	0.026		

[1]Significance levels for comparisons between the mean proportions of body mass which was stomach contents (arcsine units) for lactating and nonlactating females were determined by t tests.

To derive a single index value for relative food consumption between lactating and nonlactating females, we performed alternative calculations. In this case we did not simply pool data because that would not adequately account for digestion trends. Northern fur seals feed primarily at night or in the early morning hours (Fiscus et al. 1964; Gentry et al. in press); therefore, we considered the value at 0-3 h after sunrise (0.96; Table 2) as the relative daily quantity of stomach contents for nonlactating seals. Feeding more than once a day to satisfy only energy needs of maintenance and routine activity should be done by all fur seals, and would already be included in these results (Table 2) when the inherent relative rate of digestion is examined. However, lactating females require additional food intake for milk production, and we added an increment (0.12) to the value observed at 0-3 h after sunrise (1.56; Table 2) to calculate an adjusted index of 1.68% of body mass. This incremental value was derived first by calculating the rate of decrease between data values for partially digested stomach contents at the different hourly time intervals. We assumed the rate of digestion throughout the day was the same for lactating females as that observed for nonlactating females. Next, keeping the value for lactating females at 0-3 h after sunrise (1.56) as constant, we summed the absolute value of the differences between the expected values for remaining stomach contents and the observed values in Table 2 to obtain a value of 0.12. We then calculated a value of 174% as our index of relative food intake (i.e., the ratio of 1.68 for lactating females relative to 0.96 for nonlactating females) for a typical foraging day. However, because females do not feed every day during the breeding season (Bartholomew and Hoel 1953; Peterson 1968; Gentry and Holt in press), the average daily feeding rate (adjusted for percentage of time feeding at sea) for lactating seals is 1.6 times that for nonlactating seals during July-September, i.e, the increased cost of lactation is +59.8%.

Estimated Energy and Food Requirements

Lactating and nonlactating female northern fur seals consumed the same species of prey in relatively similar proportions within their diet, when feeding in the same general area at the same time during 1958-74. Ranks of importance of prey to the diet were significantly correlated ($P < 0.05$); the percent similarity of relative prey importance by percent modified volume was 80%; and there was no significant difference in the frequency of food stomachs containing fish or squid. Being culled from the same region and for the same season, data for all adult females were pooled.

We derived a gross energy estimate of 1.40 kcal/g as the average energetic density of northern fur seal prey during July-September based on their relative dietary importance and information in the literature on their energy content (Table 3). Using the data on seal body mass (Table 1) and increased cost of lactation (+59.8%), we calculated average daily feeding rates of 18.2% (6.42 kg) and 11.4% (3.55 kg) of total body mass, respectively, for the average lactating and nonlactating adult female. This represents daily energy consumption requirements of

TABLE 3.—Relative dietary importance, energy value and average daily consumption of prey by individual lactating and nonlactating female northern fur seals (age ≥4 yr) in the eastern Bering Sea during July-September.

Prey	Relative dietary importance (%)[1]	Energy (kcal/g)[2]	Relative energy value in diet (%)[3]	Estimated average consumption			
				Biomass (kg/d)		Energy (kcal/d)	
				Lactating	Nonlactating	Lactating	Nonlactating
Pacific herring	7.67	[4]2.17	11.95	0.49	0.27	1,070	590
Salmonids	1.87	[5]2.01	2.69	0.12	0.06	240	130
Capelin	14.85	[6]1.31	14.00	0.95	0.53	1,250	690
Deepsea smelt	3.30	[7]0.76	1.81	0.21	0.12	160	90
Walleye pollock	36.11	[6]1.41	36.51	2.32	1.28	3,270	1,800
Atka mackerel	1.05	[8]1.58	1.19	0.07	0.04	110	60
Pacific sand lance	0.43	[5]1.22	0.38	0.03	0.02	40	20
Flounders	1.10	[5]1.20	0.94	0.07	0.04	80	50
Subtotal (fish)	66.38	[9]1.46	69.47	4.26	2.36	6,220	3,430
Gonatid squid	33.62	[10]1.27	30.53	2.16	1.19	2,740	1,510
Total	100.0	[9]1.40	100.00	6.42	3.55	8,960	4,940

[1]Percent modified volume of stomach contents data collected during 1958-74.

[2]For some species, data were derived from results of proximate analyses on muscle tissue composition using energetic density factors of 9.50, 5.65 and 4.00 kcal/g (gross energy), respectively for fat, protein, and carbohydrate (Watt and Merrill 1963). Data for other species were based on bomb calorimetry analyses of whole specimens.

[3]Derived by multiplying columns 1 and 2, and summing to 100%.

[4]Based on proximate analysis data for Pacific herring, *Clupea harengus pallasi*, in Bigg et al. (1978).

[5]Based on proximate analysis data for salmonids (Salmonidae); Pacific sand lance, *Ammodytes hexapterus*; and flounders (Pleuronectidae) in Sidwell (1981).

[6]Based on data from heat of combustion in analyses of whole fish specimens of capelin, *Mallotus villosus*, and walleye pollock, *Theragra chalcogramma* [Miller, L. K. 1978. Energetics of the northern fur seal in relation to climate and food resources of the Bering Sea. U.S. Mar. Mammal Comm. Rep. MMC-75/08, 27 p.]

[7]Based on proximate analysis data for deepsea smelt (Bathylagidae) in Childress and Nygaard (1973).

[8]Based on proximate analysis data for Atka mackerel, *Pleurogrammus monopterygius*, in Kizevetter (1971).

[9]Average value of prey species in diet adjusted by their relative dietary importance.

[10]Perez, M. A. 1984. Unpubl. data. Northwest and Alaska Fish. Cent. Natl. Mar. Mammal Lab., Natl. Mar. Fish. Serv., NOAA, 7600 Sand Point Way NE., Seattle, WA 98115.

8,960 kcal and 4,940 kcal for the average, individual lactating and nonlactating adult female northern fur seal during July-September (Table 3). Average postpartum females not in a lactating state would have a daily energy consumption requirement of 5,430 kcal or feeding rate of 11.0% (3.89 kg) of total body mass.

Table 3 also provides estimates for each food item of the total energy and biomass consumed daily by the average individual adult female. Lactating females each consume about 6,220 kcal/d gross energy (4.3 kg/d) of fish and 2,740 kcal/d gross energy (2.2 kg/d) of squid, and each nonlactating individual consumes about 3,430 kcal/d gross energy (2.4 kg/d) of fish and 1,510 kcal/d gross energy (1.2 kg/d) of squid. Female northern fur seals are not able to feed every day, and thus estimated consumption for the average foraging day is 8,980 kcal/d gross energy (6.1 kg/d) of fish and 3,950 kcal/d gross energy (3.1 kg/d) of squid by lactating seals, and 4,530 kcal/d gross energy (3.1 kg/d) of fish and 1,990 kcal/d gross energy (1.6 kg/d) of squid by nonlactating females.

We also calculated estimates of the total energy in biomass consumed by all adult females during July-September in the eastern Bering Sea (Table 4). Because the northern fur seal population has been declining in recent years (North Pacific Fur Seal Commission 1984) we used 80% of the estimated population values given by Lander (1981): 2.61×10^5 pregnant/postpartum and 1.19×10^5 nonpregnant adult females (age ≥4 yr). We assumed all of these seals are present in the eastern Bering Sea during this period. Because 5% of the pups born on St. Paul Island, Pribilof Islands, between 1975 and 1982 died on the rookeries during July and August (Kozloff 1985), we modified our calculations to reflect the number of postpartum females which are nonlactating. We thus estimated a total of 2.48×10^5 lactating and 1.32×10^5 nonlactating adult females (age ≥4 yr). Multiplying individual estimates by these population totals, lactating females consume an estimated collective total of 204.5×10^9 kcal gross energy (146.5×10^3 t) and nonlactating females consume an estimated collective total of 60.2×10^9 kcal gross energy (43.1×10^3 t) of food. Therefore, all adult female northern fur seals consume an estimated collective biomass of 189.6×10^3 t with a gross energy value of 264.7×10^9 kcal during July-September, of which 69.4% of this energy (183.7×10^9 kcal; 125.9×10^3 t) are fish and 30.6% (81.0×10^9 kcal; 63.7×10^3 t) are squid.

TABLE 4.—Estimated energy value and consumption of fish and squid by the total population of lactating and nonlactating female northern fur seals (age ≥4 yr) during July-September (92 days).

		Lactating females			Nonlactating females		
		Individual average	Total seasonal consumption by population (2.48 × 10^5)		Individual average	Total seasonal consumption by population (1.32 × 10^5)[2]	
Prey	Energy (kcal/g)[1]	consumption (kg/d)[1]	Biomass (× 10^3 t)	Energy (× 10^9 kcal)	consumption (kg/d)[1]	Biomass (× 10^3 t)	Energy (× 10^9 kcal)
Fish	1.46	4.26	97.2	141.9	2.36	28.7	41.8
Squid	1.27	2.16	49.3	62.6	1.19	14.4	18.4
Total	1.40	6.42	146.5	204.5	3.55	43.1	60.2

[1]From Table 3.
[2]Includes postpartum females that fail to lactate.

DISCUSSION

The food consumption data presented in Table 2 were based on partially digested stomach contents, and thus underestimate the actual feeding rates of adult female northern fur seals. It is apparent from these data that lactating seals obtain most of their energy needs by filling their stomachs slightly more than the nonlactating seals early in the day and by eating additional food later in the day. Any female, whether lactating or not, may eat more than once during the day, as captive northern fur seals often do (Spotte 1980). Females must feed more than once during the 24-h period (on those days when they are able to feed) to meet their daily food requirements because the maximum observed stomach contents by percentage of body mass during July-September 1958-74 were 13.8 and 8.2%, respectively, for lactating and nonlactating females (Perez[3]), which are less than their predicted feeding rates. In addition, digestion does vary among individual seals and with the type and amount of prey eaten (Bigg and Fawcett 1985). However, the data in Table 2 should be typical of the relative relationship between lactating and nonlactating females if actual feeding rates could be measured for free-ranging seals.

Lactating northern fur seals were estimated to consume 8,960 kcal/d (gross energy), of which 3,520 kcal/d (gross energy) represent the additional intake of food related to lactation. Energy expenditures for maintenance and routine activity not directly attributable to lactation were estimated to be 5,440 kcal/d (gross energy). This estimate is about 5.4 times the amount predicted (1,010 kcal/d metabolizable energy or 49.0 W) for basal metabolism by the relationship between metabolic rate (MR) in watts (W) and body mass (M) shown by Kleiber (1961) (MR (W) = 3.39 $M^{0.75}$).

These estimates are not typical of energy expenditure during the first week (7.4 d average) postpartum, a period during which the parturient female does not feed. Lactating seals must metabolize their energy from fat reserves during this period (including the day before parturition when they usually do not feed, although we considered only the postparturition period). The loss in body mass (Table 1) in postpartum females following parturition accounts for some of this metabolism of energy from fat reserves. This loss includes about 0.6 kg (12% of pup mass as in harp seals, Lavigne and Stewart 1979) of placental matter and 3.3 kg (7% preparturient female mass) of amniotic and other fluids during parturition (Costa and Gentry in press). There is a calculated net mass loss of 3.2 kg. Loss of body water, as has been reported for some mammals, e.g., cattle (Degen and Young 1980) is also probably part of this loss. In addition, this loss includes the utilization of fat reserves to satisfy energy requirements for lactation (Sadleir 1969) during the first few days of the pup's life, a period when parturient females remain on shore and do not feed (Bartholomew and Hoel 1953; Peterson 1968; Gentry and Holt in press).

Our estimate of net mass loss, presumably through fat metabolism, is an underestimate because it was derived from mean body mass data from seals taken at sea, and, therefore, includes lactating animals which probably regained some body mass after their first foraging trip at sea. Costa and Gentry (in press) measured an average of 8.75 kg of mass loss, presumably by tissue metabolism and water loss, prior to the female's initial departure to sea, after which they gained additional body mass. This situation is analogous to that in gray seals. The gray seal does not feed during its entire 18-d lactation period from parturition to weaning (Amoroso and Mat-

[3]Perez, M. A. 1981. Unpubl. data. Northwest and Alaska Fish. Cent. Natl. Mar. Mammal Lab., Natl. Mar. Fish. Serv., NOAA, 7600 Sand Point Way NE, Seattle, WA 98115.

thews 1951, 1952) and over 80% of the female's stored energy reserves are used to feed their pup (Fedak and Anderson 1982).

We conducted similar analyses of data comparing pregnant and nonpregnant adult females (age ≥4 yr) during June-July, but we did not find any significant difference in relative feeding rates. We, therefore, conclude that the onset of the lactation process, and not pregnancy, initiates increased feeding behavior in parturient fur seals. Pregnant northern fur seals presumably consume more food than required by nonpregnant females (i.e., more than that simply required as a function of body mass). This would be necessary for growth of the fetus, especially during winter and spring months when they are in the North Pacific. This conclusion was based on a preliminary examination of the pelagic fur seal data, although the results were not statistically conclusive. Female northern fur seals probably also store energy in fat reserves for the stresses of birth and the first week of lactation. Nevertheless, any additional food intake required by pregnant females is substantially less than that of lactating seals.

We believe lactating females may reduce their need for additional food intake during the last month prior to weaning of pups because we did not find a significant difference in food consumption between lactating and nonlactating females during October; however, data were few. Weaning does not occur until late October or early November when females abandon their pups; the mean date of weaning is about 2 November (Peterson 1968). It should be noted that births occur over at least a 30-d period (Peterson 1968), and weaning of individual pups will likewise occur over a similar time frame. It is thus possible that pups born earlier will quit nursing earlier than those born later in the season. The total lactation period is about 3-5 mo. Therefore, the feeding rate relationships and energy estimates presented in this paper should typify those during the first three months of lactation only, and not necessarily during July-September.

We assumed that all postpartum females taken during 1958-74 were lactating. We believe that this assumption does not significantly affect our results because only a small percentage of the postpartum females fail to lactate or terminate lactation for one reason or another (such as still birth or death of the pup). Therefore, our estimate of the difference in consumption between lactating and nonlactating females is a conservative indicator of the magnitude of this ratio. This is because inclusion of postpartum females that did not lactate would have decreased the mean value of stomach contents for the lactating group.

Individual northern fur seals show variations in their feeding locations. Differences may occur over location and time. For example, lactating females may travel great distances, e.g., at least 160 km from the Pribilof Islands (Perez[4]), during their sea trips in search of food, and they may dive up to 200 m (Gentry et al. in press) to catch prey. There are, of course, differences in availability (e.g., walleye pollock, *Theragra chalcogramma*, Smith and Bakkala 1982) and energetic density (e.g., Pacific herring, *Clupea harengus pallasi*, Bigg et al. 1978; deepsea smelt, Bathylagidae, Childress and Nygaard 1973) of prey by season, region, and depth. The 95% C.I. for the importance of fish biomass in the fur seal diet in the Bering Sea is 64.0-68.6% (Perez and Bigg[5]). Therefore, the estimated quantity of fish and squid consumed, and their relative energy contribution, may vary ±5%.

It should also be stressed that the estimates presented in this paper also depend heavily on metabolic rate information for adult females which we obtained from the literature. Individual variations among seals will cause differences in results obtained from several experiments, and future research may provide somewhat different metabolic rates. Should feeding rates be revised substantially, then the magnitude of energetic estimates from these data will be affected in a corresponding direction. However, the relative ratio of food consumption between lactating and nonlactating females during the breeding season will be unaffected, and remain about 1.6. We suggest the need for further studies on feeding behavior and energetics of lactating females and pups prior to weaning.

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[4]Perez, M. A., Northwest and Alaska Fisheries Center National Marine Mammal Laboratory, National Marine Fisheries Service, NOAA, 7600 Sand Point Way NE, Seattle WA 98115, pers. observ., 1984.

[5]Perez, M. A., and M. A. Bigg. 1984. Food habits of northern fur seals (*Callorhinus ursinus*) off western North America. Unpubl. rep., 67 p. Northwest and Alaska Fish. Cent. Natl. Mar. Mammal Lab., Natl. Mar. Fish. Serv., NOAA, 7600 Sand Point Way NE, Seattle, WA 98115.

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ARRIVAL OF NORTHERN FUR SEALS, *CALLORHINUS URSINUS*, ON ST. PAUL ISLAND, ALASKA

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ABSTRACT

The age-specific arrival times and relative numbers of northern fur seals, *Callorhinus ursinus*, on St. Paul Island, Alaska, were determined from an analysis of kill data collected during 1956-82, and a review of the fur seal literature. Arrival times differed by sex, age, and reproductive state. Arrival took place progressively earlier with age in young males and females. Most males age ≥6 arrived by late June, while most males age 5 arrived by late June to early July, those age 4 by mid-July, those age 3 by late July, those age 2 by mid- to late August, and those age 1 by late September to early October. Females tended to arrive later than males of the same age. Nonpregnant females age ≥3 arrived by mid-August, while those age 2 arrived by mid- to late September, and females age 1 by October to early November. Pregnant females age ≥4 arrived mainly by mid-July, about 1 month before nonpregnant females of the same age. For both sexes, the number of seals returning increased between age 1 and age 3. Both sexes appeared to stop arriving earlier and in larger numbers at about the age of sexual maturity. The process of gradual maturation may play a role in inducing a cohort to undertake the return migration at earlier times with age, and to cause a greater proportion to return.

The northern fur seal, *Callorhinus ursinus*, inhabits the North Pacific Ocean mainly between lat. 32°N and 60°N (Fiscus 1978; King 1983). The species is migratory, being pelagic and widely dispersed in winter, and gathering on rookeries to give birth, mate, nurse, and rest in summer. Rookeries occur along the Asian coast on Robben, Kurile, and Commander Islands, and along the North American coast mainly on the Pribilof Islands and on San Miguel Island. The presence of large numbers of animals on Robben Island, Commander Islands, and the Pribilof Islands has allowed an annual commercial kill for pelts over many years.

The Pribilof Islands, in particular St. Paul Island and St. George Island has the largest stock of seals, numbering currently about 0.9 million (North Pacific Fur Seal Commission 1984a). The species has been harvested there almost every year since discovery in 1786 (Roppel and Davey 1965; Roppel 1984). Over the years, fishery managers learned to adjust the kill quite specifically for seals of a particular age and sex by making use of the arrival sequence of migrants and their preferences for haul-out sites. For example, Russians in the early 1800's took juvenile males on hauling grounds, and left the breeding adults and pups undisturbed on nearby rookeries. Americans in the late 1800's knew that the largest, and thus oldest, juvenile males arrived before small males (Jordan and Clark 1898). Following the discovery in 1950 that teeth could be used for aging, the kill was refined further to focus on 3- and 4-yr-old males. Although the kill has been directed primarily at young males since the early 1900's, females were taken during a herd reduction program from 1956 to 1968.

Behavioral studies on the Pribilof Islands have documented the arrival times for broad population categories, such as adult and juvenile males, and pregnant females (Jordan and Clark 1898; Bartholomew and Hoel 1953; Peterson 1965, 1968; Gentry 1981). However, these studies could not determine the age-specific arrival times because no method was available to distinguish the age of the live animals being observed. The widely accepted arrival sequence was for bulls to arrive on land first, followed by progressively younger males, progressively younger pregnant females, and later by mostly young nonpregnant cows (Kenyon and Wilke 1953; Fiscus 1978). This arrival sequence was deduced from preliminary examinations of the age and sex composition of commercial kills and from the arrival times of tagged individuals and to some extent from differences in body size, at least for the 1- and 2-yr-olds. There are no published analyses that describe age-specific arrival times, although some unpublished reports give information on arrival times.

In this study, I determine the arrival times for seals of each age, sex, and reproductive condition on hauling grounds and rookeries of St. Paul Island, the largest of the Pribilof Islands. The study is based

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mainly on an analysis of seasonal changes in the number of animals killed of each age during harvests. I examine the evidence for arrival times by order of decreasing age within each sex, and compare the relative numbers returning for each age of young seals. The published and unpublished literature on northern fur seals is reviewed for information on arrival times and abundance. The relationship between arrival schedules, relative number returning, and onset of sexual maturity is discussed.

METHODS

The kill data from St. Paul Island used in this study were collected during 1956-82 by the National Marine Mammal Laboratory, National Marine Fisheries Service, Seattle. Most data up to 1979 were listed by Lander (1980), who noted the method of data collection and the number killed by age, sex, date, and location. Kozloff (1981[2], 1982, 1983) listed the data collected during 1980-82. Abegglen et al. (1956, 1957, 1958, 1959) determined the age-specific pregnancy rates of females killed during 1956-59. These authors considered a female to be pregnant when parous (carrying a term fetus), or recently postpartum (lactating or uterus involuting). They did not separate females into these two categories, or determine whether postpartum females were carrying a new conceptus.

Almost all males and females were killed on hauling grounds rather than on rookeries. No commercial kills for males took place on rookeries, and only a few took place for females. Typically, the kill of both sexes on hauling grounds was made between late June and mid-August. It consisted of a series of consecutive 5-d circuits, or rounds, of all hauling ground sites. During each round, a crew undertook one killing operation at each site, and killed all seals present of a particular sex and length. The body length limits for harvesting were set in inches (in) from nose to tip of tail, or from nose to base of tail. I converted all lengths to cm and standard length, using 1 in for tail length. Lander (1980) and the North Pacific Fur Seal Commission (1984b) noted the annual changes in management practices on St. Paul Island. The changes included variations in body length limits, kill dates, quotas, kill locations, and special kills for sex and age. I used only data that were collected under comparable management restrictions.

[2]P. Kozloff (editor). 1981. Fur seal investigations, 1980. NWAFC Processed Rep., 96 p. National Marine Mammal Laboratory, National Marine Fisheries Service, NOAA, Seattle.

Probit plots of age-specific cumulative length frequencies were used to determine the percentage of males and females of each age present in the kill for each set of length limits. Sufficient age-length data were not available for the plots from kills made on St. Paul Island, but were available from samples collected pelagically for research purposes by the United States and Canada under the terms of the North Pacific Fur Seal Commission. These data are on file at the Pacific Biological Station, Nanaimo, and at the National Marine Mammal Laboratory, Seattle. The age-length data used were from seals collected near St. Paul Island during June-August 1958-74. The lengths of females used were those of postpartum and nonpregnant seals, the main categories of females killed on land.

I assumed that seals were arriving on St. Paul Island when the number killed increased in successive rounds and that arrival was completed when the number killed reached an asymptote. These assumptions were valid only under certain circumstances. One was that all seals encountered of a designated sex and length were killed, which was the case. Another was that the number of seals hauled out, and thus available for killing, was a constant proportion of the number alive through the harvest season. The assumption seems reasonable in that Gentry (1981) estimated an average of about 19% of marked juvenile males were ashore at any one time on St. George Island. Finally, the proportion of a particular age and sex killed during each year must have been sufficiently small so as not to have substantially reduced cohort size, and thus altered the trend in numbers killed by round. This qualification was probably true for all ages, except perhaps for 4-yr-old males. Lander (1981) estimated the harvest utilization rate of males on St. Paul Island to be only 2.8% for age 2, 40.3% for age 3, 14.7% for age 5, but 57.3% for age 4. Escapement rates of females from the commercial harvest were not calculated, but were probably high. The females killed were mainly of ages 3 and 4 with the largest annual take for age 3 in the years studied being 9,700, and for age 4 being 6,300. These figures compared with about 55,000 and 48,000, respectively, for females present in the whole population, based on Lander's (1981) life table for the species.

The number killed of each age up to the last day of each round for each year was plotted to describe the seasonal change in numbers killed. For males, the most common last-day dates for each round were in the series of 5-d rounds ending between 1 July and 5 August. For years in which the dates for last-day rounds differed from this series, the number of

males killed was interpolated from the annual plots, so as to standardize the number killed by date. The mean number of males killed, and standard error of the mean, were determined for each date of the last-day of rounds. During 1965-72, a kill of males sometimes took place twice at a haul-out site in one round, but was missed at this site in the preceding or following round. In these cases, one of the two kills was selected randomly and transposed to the other round. Occasionally, sites were visited extra times without being missed in the adjacent round. These data were omitted.

The kill data used for females on hauling grounds were from years in which the kills on rookeries and hauling grounds were recorded separately, and in which the pregnancy rates were noted. Such kills took place only during 1956-59. These kills were made during the 5-d rounds with the last-day dates between 1 July and 20 August. The only kills on rookeries for which pregnancy data could be used were in 1956 and 1957. On 1-6 July 1956, a kill was made on Polivina rookery. All kills made in the region of this rookery on 1-21 July 1957 were in fact made only on the rookery (A. Roppel[3]). The number of females killed on rookeries was set by quota, rather than by all available animals being taken, as on hauling grounds. No body length limits were imposed on the kill of females on rookeries in 1956 and 1957.

To determine the relative number of each age that returned to St. Paul Island, I reviewed the largely subjective comments on abundance given in the literature, and also compared the number killed when arrival was believed to have been completed. For the latter, the only data used were from years when body length limits included at least 50% of the individuals of the relevant age and when the total number of living animals of a particular age did not change substantially between years. The main change in herd size was between 1956 and 1959, when pup production on St. Paul Island decreased by about 27% due to the killing of adult females during the herd reduction program (York and Hartley 1981; Fowler 1982). Pup production changed little between 1960 and 1980, although declined slightly in 1981-82. The cumulative effect of harvesting a cohort over several years was considered when comparing the relative number of each age killed. The relative numbers of females of each age killed between 1956 and 1959 were biased slightly downward with time by the herd reduction program during the intervening years. The bias was only slight because of the years and ages selected for analysis, the lack of time for the herd reduction program to have potentially changed age distribution, and the fact that most seals ages 1 and 2 remained at sea.

[3]A. Roppel, Northwest and Alaska Fisheries Center, National Marine Fisheries Service, NOAA, 7600 Sand Point Way N.E., Seattle, WA 98115, pers. commun. July 1983.

RESULTS

Effect of Body Length Limits

The lower length limit of 107 cm for males included essentially no individuals age 1, few age 2, but most of those ≥3 yr (Table 1). The upper length limit varied by year, with the smallest upper limit including a few ≥4 yr, and the largest, a few ≥6 yr. I used kill data collected from the years 1969-82 to describe arrival times and relative numbers of males ages 1 and 2. Data from the years 1962-82 were used to describe the arrival time and relative number of 3-yr-olds. For males ≥4 yr, the relative numbers returning by age could not be compared with one another, or with younger males, because of the cumulative reduction in the size of a cohort by the harvest, and the exclusion of seals by upper length limits. I used data from the years 1963-72 and 1980-82 to describe the arrival schedule for age 4, and 1964-71 for ages 5, 6, and ≥7.

The lower length limit of 104 cm for females included most individuals ≥4 yr, while the upper length limit of 116-117 cm included mostly ≤5 yr. Data collected in 1956 were used to describe the arrival schedules for females ≥4 yr, and 1958-59 for those ≤5 yr. The number of females killed at age 3 during 1959 was not used due to an unusually low pup survival in 1956 (Abegglen et al. 1959; Lander 1979).

Arrival of Males on Hauling Grounds

1-Year-Olds

No yearling males were taken in the kill by 5 August, and thus none were likely to have been on hauling grounds up to this time. However, few yearling males apparently go to hauling grounds. Osgood et al. (1915) and Roppel et al. (1965a) indicated that yearlings of both sexes preferred rookery edges, near cows and pups, and only occasionally went to hauling grounds (see section on Arrival of Males on Rookeries).

2-Year-Olds

Very few 2-yr-old males arrived by 1 July (Fig.

TABLE 1.—Percent of each age included in standard length restrictions for kills of male and female northern fur seals on hauling grounds. Percentages determined from Probit plots of age-length cumulative length frequencies of seals collected at sea near St. Paul Island by the United States and Canada. Sample sizes are in parentheses.

Length limit (cm)	Years	Age (yr) 1	2	3	4	5	6	≥7
		Males						
		(24)	(166)	(251)	(117)	(48)	(20)	(43)
107-119	1956-58, 1960	1.6	27.7	71.0	44.2	5.0	3.0	0.0
107-121	1959	1.6	27.9	76.5	55.7	8.3	4.0	0.0
107-124	1961-63	1.6	28.0	79.5	71.2	15.5	6.5	0.0
107-[1]135	1964-68	1.6	28.0	82.0	96.8	64.0	28.0	≤1.2
[1]≤135	1969-71	100.0	100.0	100.0	98.6	64.0	28.0	≤1.2
≤124	1972, 1980-82	100.0	100.0	97.5	73.0	15.5	6.5	0.0
≤117	1973-75	100.0	99.2	82.0	35.0	3.0	1.5	0.0
≤119	1976-79	100.0	99.5	86.0	40.0	4.0	2.0	0.0
		Females						
		(18)	(69)	(297)	(465)	(301)	(136)	(530)
≥104	1956	0.0	16.0	48.0	89.0	97.0	99.4	≥99.9
≤116	1958	100.0	99.8	98.4	80.0	54.0	31.5	≤12.0
≤117	1959	100.0	99.9	99.0	84.0	63.0	40.0	≤16.0

[1]Upper body size was the presence of a mane. A. Roppel (National Marine Mammal Laboratory, National Marine Fisheries Service, NOAA, Seattle, WA 98115, pers. comm. July 1983) felt that the mane developed at a body length of about 135 cm.

1). Numbers began to increase in early July and continued to increase up to 5 August. This age group began to arrive earlier than the yearlings. Osgood et al. (1915) observed the first branded 2-yr-old individuals on 12 June, about 1½ mo before the first branded yearling males on rookeries. As found in the current study, Kenyon and Wilke (1953) noted that 2-yr-olds were quite common by the end of July, and after 1 August became increasingly abundant.

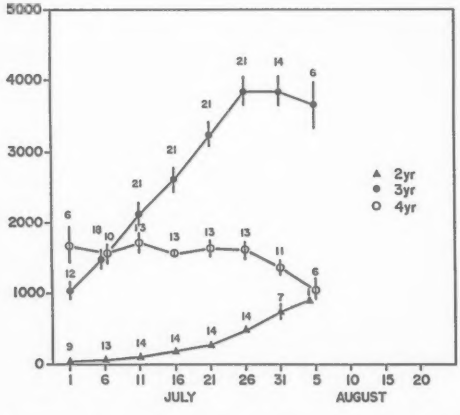

FIGURE 1.—Mean number, and standard error, of northern fur seal males killed of age 2-4 on hauling grounds of St. Paul Island, by date. Data from Lander (1980) and annual reports of the National Marine Mammal Laboratory, Seattle. Number of years of data for each date indicated above means.

The date of peak numbers, and thus the date when most arrived, was probably after early August. The date when most would have arrived may be determined by assuming that the interval between the time when seals clearly began to increase in number and the time when essentially all seals had arrived was the same for 2-yr-olds as for bulls and cows. Observations by Peterson (1968) suggested that this interval was about 1-1½ mo for bulls and pregnant females. Because the number of 2-yr-old males began to increase in early July, the arrival time for most was probably mid- to late August. A similar arrival time was also indicated by subtracting 1-1½ mo, the interval separating the first sightings of tagged yearlings and 2-yr-olds, from the arrival time of late September to early October for yearling males on rookeries.

The number of 2-yr-olds returning appeared to be greater than that for yearlings, but less than that for 3-yr-olds. Roppel (fn. 3) felt that more 2-yr-old males returned than yearling males, and Kenyon et al. (1954) noted that many 2-yr-olds remained at sea.

3-Year-Olds

The 3-yr-olds were already quite abundant by 1 July and reached a peak in numbers by late July (Fig. 1), suggesting that arrival was completed by late July. Kenyon and Wilke (1953) similarly noted the maximum number of 3-yr-olds on hauling grounds was after mid-July. This age group

appeared to have the largest number of males returning.

4-Year-Olds

The number of males killed of age 4 remained essentially constant during July, except for a decrease in late July (Fig. 1). Although no distinctive peak in numbers was evident, several factors suggest the main arrival was probably completed by mid-July. First, the number killed in the first round (i.e., up to 1 July) was likely to have been too large relative to later rounds because of an accumulation of males that arrived before the kill began. This situation was most obvious for kills of males ages 5 and 6 (Fig. 2), but also could have existed to some extent for the kill of males ages 2 and 3. For ages 2 and 3, the accumulation would not have been as obvious because the main arrival time was after kills began. Secondly, the true peak in number killed of 4-yr-olds was probably flattened by the high harvest utilization rate of this age. Finally, an examination of the trend in numbers killed by round for individual years indicated the seasonal pattern was quite variable, ranging between that noted for males age 3, and that for males age 5. For example, the arrival time for 4-yr-olds in 1971 was similar to that seen for the typical 3-yr-olds; it was similar for the typical 5-yr-olds in 1968; and in 1980 it was intermediate, with a distinctive peak in mid-July. Such variations tended to dampen the peak. Kenyon and Wilke (1953) remarked that the maximum number of males older than 3 yr arrived before mid-July. Fewer age-4 males returned than age-3 males, probably due to the large kill at age 3.

5-Year-Olds

Most 5-yr-olds appeared to have already arrived by early July (Fig. 2). However, as noted for 4-yr-olds, the kill by 1 July was probably large relative to the number killed in later rounds. Most males probably arrived by late June to early July, assuming the time in peak numbers of 5-yr-olds was earlier than mid-July, but not earlier than for territorial bulls (≥7 yr) on rookeries. Fewer 5-yr-olds returned than 4-yr-olds because of the large kill of males at age 4.

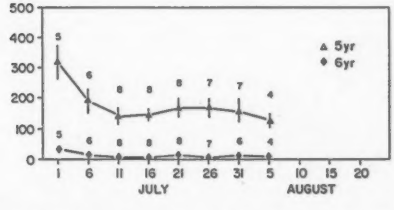

FIGURE 2.—Mean number, and standard error, of northern fur seal males killed of age 5-6 on hauling grounds of St. Paul Island, by date. Data from Lander (1980) and annual reports of the National Marine Mammal Laboratory, Seattle. Number of years of data for each date indicated above means.

6-Year-Olds

As with 4- and 5-yr-olds, the first kill was likely too large. Most 6-yr-olds probably arrived by late June. Gentry (1981) tagged juvenile males on hauling grounds of St. George Island in 1977 and counted them during late May to mid-August 1980. Although the ages were not known with certainty, the most common age in 1977 was likely 3 yr, with a range of 2-5 yr (R. Gentry[4]), and thus most males in 1980 were probably 6 yr of age. His counts indicated numbers began to increase in late May, reached a peak on 19-28 June 1980, and declined thereafter.

≥7-Year-Olds

No males older than 6 yr of age were taken in the annual kills on hauling grounds. This was because the upper length limits excluded these ages from kills, and because many males of these ages go to rookeries for breeding rather than to hauling grounds.

Arrival of Males on Rookeries

1-Year-Olds

Behavioral studies suggest most yearling males probably arrived on rookeries by late September to early October, and the number returning was the smallest of any age group of males. Osgood et al. (1915) reported that branded male yearlings were rarely seen between late July and mid-August but became more numerous later, although they always remained small in number. Kenyon and Wilke (1953) mentioned yearlings of unspecified sex returned principally in September to November, and that only a few individuals were involved. Using counts of tagged yearlings seen on rookeries between 17 September and 17 October, Roppel et al. (1965a)

[4]R. Gentry, Northwest and Alaska Fisheries Center, National Marine Fisheries Service, NOAA, 7600 Sand Point Way N.E., Seattle, WA 98115, pers. commun. February 1984.

suggested that the largest number of yearlings of unspecified sex was present on 27 September to 11 October. These animals were predominantly males, as indicated by the recorded sex ratio of 84% males in a sample of 356 yearlings seen during 1961-65 (Roppel et al. 1965a, 1965b, 1966). Osgood et al. (1915) noted all yearlings examined during his study were males. Surveys by Abegglen et al. (1961) indicated very few yearlings of either sex were present on rookeries after early November.

≥7-Year-Olds

Essentially all males present on rookeries during the pupping season were bulls (Jordan and Clark 1898). According to Johnson (1968), the age of such bulls would have been ≥7 yr. Peterson (1965, 1968) noted that bulls began to arrive on rookeries in mid-May, reached peak numbers by late June, and declined in numbers after mid-July. No data exist on whether old bulls arrived before young bulls.

Arrival of Females on Hauling Grounds

Pregnant, ≥4 Years

Very few females younger than 4 yr give birth (Lander 1981). Pregnant females age ≥4 were rarely taken on hauling grounds during July, but were increasingly common during 1-15 August (Fig. 3). Using the trend in the number of 4- and 5-yr-olds killed after 15 August, most pregnant females probably arrived by mid-August. Because essentially all pregnant females gave birth in July, the pregnant females killed on hauling grounds during August would have been postpartum. An examination of the median dates for collection of pregnant females suggested that arrival times on hauling grounds of age ≥4 did not differ among ages (Table 2).

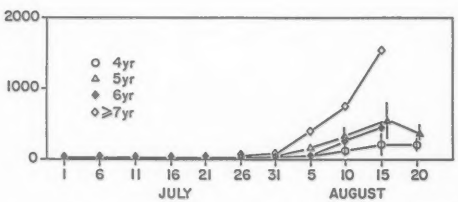

FIGURE 3.—Mean number, and range, of pregnant females of northern fur seal killed of age ≥4 on hauling grounds of St. Paul Island, by date. Data from Lander (1980) and annual reports of the National Marine Mammal Laboratory, Seattle.

Nonpregnant

1-YEAR-OLDS.—As with yearling males, yearling females apparently preferred rookeries to hauling grounds (Jordan and Clark 1898; Roppel et al. 1965a). No yearling females were taken on hauling grounds during the commercial kill for females up to 20 August.

2-YEAR-OLDS.—Jordon and Clark (1898) and Osgood et al. (1915) suggested 2-yr-old females also preferred rookeries to hauling grounds. However, a few were taken on the hauling grounds during the harvest for females. Numbers began to increase in mid-August (Fig. 4), and thus increases began about 1 mo later than males of the same age. Assuming a 1-1½ mo interval for essentially all animals to arrive, as assumed for 2-yr-old males, then 2-yr-old females probably arrived by mid- to late September.

≥3-YEAR-OLDS.—Very few nonpregnant females ≥3 yr were taken on hauling grounds in July, but many were present by 15 August (Figs. 4, 5). Based on the trend in the number of females killed at 3-5 yr, the arrival of ages ≥3 yr was essentially completed by mid-August. Support for this conclusion comes from Peterson (1965, 1968), who counted

TABLE 2.—Median dates of collection of pregnant and nonpregnant females of northern fur seals taken during 1956, 1958, and 1959 on hauling grounds of St. Paul Island. All dates are in August. Data from annual reports of the National Marine Mammal Laborabory, National Marine Fisheries Service, NOAA, Seattle.

		Age (yr)							
Year	State	3	4	5	6	7	8	9	≥10
1956	Pregnant	—	11	11	9	11	10	10	9
	Nonpregnant	12	11	11	10	11	10	10	9
1958	Pregnant	—	9	9	9	8	10	15	10
	Nonpregnant	13	11	10	10	8	10	10	8
1959	Pregnant	—	13	12	12	12	12	12	13
	Nonpregnant	14	13	13	12	12	13	11	12

"nonbreeders" on hauling grounds and the inland edges of rookeries. "Nonbreeders" were thought to consist of idle females and young males. He observed a sharp increase in numbers in early August and that most arrived by mid-August. The current study indicated the female component of Peterson's "nonbreeders" were mainly nonpregnant females, plus a few postpartum females. Abegglen et al. (1956) noted an increase in the number of seals on hauling grounds and rookery edges between 15 August and 4 September. While this increase may have resulted from a continued influx of nonpregnant females at ⩾3 yr, it may also have been due, at least in part, to the arrival of some 2-yr-old males and females.

The increase in number of nonpregnant females during August consisted primarily of 3- and 4-yr-olds. A comparison of the median dates for collection of nonpregnant females at ⩾3 yr on hauling grounds suggests that arrival times were similar for each age (Table 2).

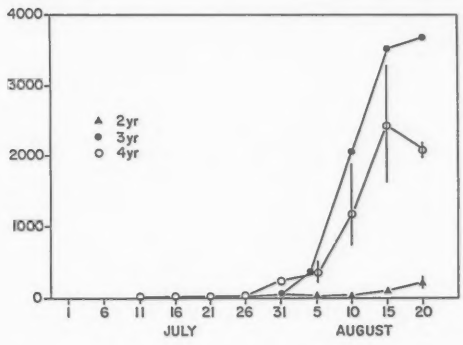

FIGURE 4.—Mean number, and range, of nonpregnant females of northern fur seal killed of ages 2-4 on hauling grounds of St. Paul Island, by date. Data from Lander (1980) and annual reports of the National Marine Mammal Laboratory, Seattle.

Arrival of Females on Rookeries

Pregnant, ⩾4 Years

Females gave birth on St. Paul Island during 15 June to 10 August, with about 90% of all births completed by 20 July (Bartholomew and Hoel 1953; Peterson 1965, 1968). The general belief that pregnant females arrived by order of decreasing age apparently originated from Wilke (1953). He collected 571 females on rookeries from 15 June to 4 September and showed the median date of collection for each age became progressively earlier with age. For example, the median collection date for females at ⩾10 yr was 7 July, while that for females at 3 yr was 23 August. However, Wilke did not separate pregnant and nonpregnant females in his calculations. The large shift in median dates probably resulted mainly from an influx of young nonpregnant females on rookeries during August, as took place on hauling grounds.

An analysis of arrival times for pregnant females of each age should not include seals that are nonpregnant. Such an analysis can be made using data collected by Wilke between 15 July and 22 July 1953 (Table 3). Although Wilke did not record pregnancy

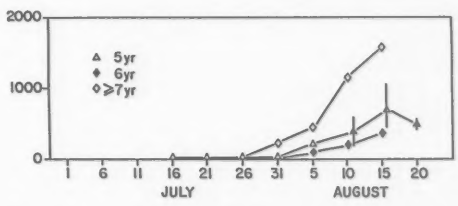

FIGURE 5.—Mean number, and range, of nonpregnant females of northern fur seal killed at age ⩾5 on hauling grounds of St. Paul Island, by date. Data from Lander (1980) and annual reports of the National Marine Mammal Laboratory, Seattle.

TABLE 3.—Median dates of collection of northern fur seal females on rookeries of St. Paul Island during 17 June to 22 July 1953. Data from Wilke (1953) and the current study.

Date	Number collected by age							
Age (yrs):	4	5	6	7	8	9	⩾10	*n*
17 June	0	2	2	1	0	0	20	25
22 June	1	0	7	3	2	2	22	37
27 June	0	2	3	1	1	3	26	36
2 July	0	4	5	7	5	5	23	49
7 July	0	2	6	3	3	6	20	40
12 July	1	3	5	1	1	0	2	13
17 July	2	2	5	3	5	5	21	43
22 July	3	9	8	7	6	1	16	50
Median date	16 Jul	10 Jul	6 Jul	4 Jul	9 Jul	3 Jul	29 Jun	

rates for this sampling period, the rates were probably 90-100%, as will be shown later on rookeries for the period 1-21 July. A comparison of median collection dates suggests arrival may have taken place slightly earlier with increasing age, but no clear shift in arrival times was evident, as previously believed. Unfortunately, the true age-specific arrival times of parous females cannot be determined readily from these data. The main difficulty is that the pregnant females used in the analysis included not just parous seals, but postpartum seals as well. Postpartum seals usually remain on land for 2 d, then go to sea to forage for 8 or 9 d, and repeat this pattern about 10 times throughout the nursing period (Peterson 1958; Gentry and Holt in press). The potentially complex effect that returning postpartum females could have on the trend in the number of parous females arriving of a particular age must be considered. Other difficulties were the small sample sizes, and the fact that the sample sizes taken on each date did not reflect the increase in numbers on rookeries. At this time, while a slight shift in arrival times of parous females may exist with age, more research is needed for confirmation.

Nonpregnant

1-YEAR-OLD.—Jordan and Clark (1898) felt yearling females did not arrive on rookeries before September. As noted earlier for yearling males, Kenyon and Wilke (1953) felt yearlings returned to the Pribilof Islands mainly during September to November, and only a few individuals were involved. The date of arrival for most yearling females is unclear, although it is probably after yearling males, during October to early November. Only a small number of yearling females had arrived by late September to early October compared to males. However, they arrived presumably no later than early November, because few yearlings were present on the rookeries after that time.

2-YEAR-OLDS.—The arrival of 2-yr-old females on rookeries began in August, a similar time to that seen on hauling grounds. Branding studies by Osgood et al. (1915) suggested a few individuals began to arrive about one month after males. The first branded 2-yr-old female was seen on 19 July compared to 12 June for males age 2. Thus, arrival was probably completed also a month later than males, by mid- to late September. Jordan and Clark (1898) reported that 2-yr-old females began to increase in numbers by about 1 August, while Kenyon and Wilke (1953) noted they did not begin until late August, and the current study suggested arrival on hauling grounds began in mid-August. Kenyon and Wilke (1953) believed the largest number were present in October, slightly later than suggested by the current study. Based on the comments by Kenyon and Wilke (1953) and Kenyon et al. (1954), fewer 2-yr-olds returned than 3-yr-olds, but more 2-yr-olds returned than yearlings.

≥4-YEAR-OLDS.—A total of 1,533 females were collected on rookeries during 1-6 July 1956 and 1-21 July 1957, a period covering the main pupping season. All females were ≥4 yr of age. Of these, only 2% were nonpregnant, a low rate compared to 31% nonpregnancy for the population as a whole, based on the life table derived by Lander (1981). The low rate likely resulted from the small number of nonpregnant females on the rookeries, as was found on

TABLE 4.—Summary of the times of arrival and relative numbers for males and females of northern fur seal rookeries and hauling grounds of St. Paul Island, based on the current study and a review of the literature.

Sex	Site[1]	State[2]	Age (yr)	Arrival time[3]	Abundance
Male	R		1	late Sept. to early Oct.	few
	HG		2	mid- to late Aug.	2 yr > 1 yr
	HG		3	late July	3 yr > 2 yr
	HG		4	mid-July	—
	HG		5	late June to early July	—
	HG		6	late June	—
	R		≥7	late June	—
Female	R	NP	1	Oct. to early Nov.	few
	HG,R	NP	2	mid- to late Sept.	2 yr > 1 yr
	HG	NP	≥3	mid-Aug.	3 yr > 2 yr
	HG	P	≥4	mid-Aug.	—
	R	P	≥4	mid-July	—

[1]R = rookery; HG = hauling grounds.
[2]NP = nonpregnant; P = pregnant.
[3] Date when essentially all seals would have arrived.

the hauling grounds at this time (Figs. 4, 5). The rate was probably biased downward by the fact that nonpregnant females stayed on land for a slightly shorter period of time than nursing females. Using data given by Gentry and Holt (in press), nonnursing females appeared to stay on shore for only about 64% as long as nursing females. Nonnursing females make about half as many visits to land as nursing females, but stay about one-third longer for each visit.

A gradual increase in the nonpregnancy rate took place on Polivina rookery during early to mid-July: 1 July = 0% (n = 280), 6 July = 2% (734), 11 July = 1% (198), 16 July = 3% (148), and 21 July = 6% (173). When weighted for the shorter period of stay on land by nonpregnant females, the rates increased from 0% by 1 July to 10% by 21 July. Presumably, the increasing rate during July resulted from the arrival of more nonpregnant females age ≥4. Numbers of nonpregnant females began to increase particularly by mid-July.

DISCUSSION

Northern fur seals arriving on St. Paul Island can go first to rookeries located on beaches just above high tide, or to hauling grounds more inland. The typical arrival sequence (Jordan and Clark 1898; Kenyon and Wilke 1953; Peterson 1965, 1968) is for the bulls to establish territories for breeding on rookeries in May-June. Pregnant females arrive next on rookeries to pup, mate, and nurse in harems within the territories. Subadult males arrive mainly during the pupping season and go to hauling grounds rather than rookeries. Although young males of different sizes (i.e., ages) tend to arrive in successive waves with time, studies of marked seals (Gentry et al. 1979) indicate that arrival times of individual subadult males can be quite variable between years. In early August, harem bulls abandon their territories, and the social structure of the rookery disintegrates. Nursing cows then tend to disperse more widely on land, and nonterritorial bulls and some subadult males move on rookeries from hauling grounds. The mixing of seals between rookeries and hauling grounds after July results in less site distinction. The literature is unclear as to the arrival times of subadult and nonpregnant adult females after July, and whether these seals go first to rookeries or to hauling grounds, or go to both simultaneously. Age 2 females arrive later in the season, and go to rookeries and hauling grounds, while yearlings of both sexes arrive last, and go mainly to rookeries. Seals begin leaving St. Paul Island for the southern migration in October to November (Roppel et al. 1965a; Kenyon and Wilke 1953). Few remain on the hauling grounds after mid-October, and few on rookeries after early November.

Table 4 summarizes the age-specific arrival times and relative numbers of seals seen on rookeries and hauling grounds, based on information given in the Results. Two arrival times existed for pregnant females, one by mid-July on rookeries and the other by mid-August on hauling grounds. The second date no doubt resulted from the movement of some postpartum females from the rookeries to the hauling grounds after the harems disintegrated. Thus, the arrival time on St. Paul Island was by mid-July, rather than mid-August.

The arrival times for nonpregnant females at ≥3 yr on to St. Paul Island was less certain than for pregnant females because age-specific data on arrival times existed from hauling grounds up to mid-August, but not from rookeries after mid-July. Also it was not known whether nonpregnant females went first to rookeries or to hauling grounds. The main arrival time was probably by mid-August, as was found on hauling grounds. This was likely because nonpregnant females began to increase in numbers on rookeries in early to mid-July, and an interval of 1-1½ mo was probably needed for essentially all arrivals to be completed. Also, Abegglen et al. (1956) felt that most females on the hauling grounds during August came directly from the sea, although some came from rookeries. From the current study, some postpartum females go from rookeries to hauling grounds. Perhaps most nonpregnant females go first to the hauling grounds.

Nonpregnant females ≥3 yr arrived about 1 mo later than pregnant females. According to R. Gentry (fn. 4), marked adult females on St. George Island also arrived later when nonpregnant, although only about 10 d later. The reason for the differences in length of delay caused by nonpregnancy found in the two studies is unclear at this time. The answer may come when details of the study by Gentry are reported, or perhaps when more is known about movement patterns of adult females between rookeries and hauling grounds.

The finding that nonpregnant females arrived after pupping suggests nonpregnancy delayed the date of mating. A delay in mating has been reported previously for maturing females, but not for nonpregnant cows. Because parous females pup about 1 d after arrival, and mate 5-6 d after pupping (Peterson 1968; Gentry and Holt in press), essentially all females that pup will have mated by mid-

to late July. Assuming a similar interval between arrival and mating for nonpregnant females, most nonpregnant females would be mated by mid- to late August. Jordan and Clark (1898) stated that young females were impregnated in early August, after old females, and Abegglen et al. (1958) observed that females ages 3 and 4 bred after the harems disbanded. Also, Craig (1964) reported females ovulated for the first time in late August or September. The only evidence that I could find of late mating in a nonpregnant cow was by Osgood et al. (1915), who observed a harem bull mating a female that was "not very young" on 21 August.

A comparison of the age-specific arrival times for each sex on St. Paul Island (Table 4) largely confirms the comments by Kenyon and Wilke (1953) and Fiscus (1978) that arrival began progressively earlier with increasing age. However, the current study indicated that this phenomenon was obvious only for young ages. It was seen in nonpregnant females ages 1-3 and in males ages 1-6. Although no differences in arrival times were shown for older males and nonpregnant females, differences could exist, but would be small. The differences in arrival times became progressively less with age for males between 1 and 6 yr and apparently for females between 1 and 3 yr.

A comparison of the relative numbers returning to St. Paul Island (Table 4) suggests that progressively more males and females returned between ages 1 and 3. The cumulative effect of the kill on males of 2 and 3 yr prevented comparisons of abundance with males ≥4 yr. For females, the number of 4-yr-olds returning was probably not greater than 3-yr-olds, as suggested by the similarity in the number of 3- and 4-yr-olds killed on hauling grounds by mid-August (Figs. 3, 4). However, pregnancies complicate comparisons of abundance on hauling grounds between females 3 yr and older. Between ages 4 and 10, an increasing proportion of females become pregnant (Lander 1981) and thus go to rookeries rather than hauling grounds.

The data collected in this study suggest that, with age, young seals of both sexes arrive progressively earlier, and in progressively larger numbers. The reason for these changes in arrival schedules lies in an understanding of the mechanism that controls the migration schedule. However, little is known about this mechamism in the northern fur seal. The mechanism, if it is like that of other vertebrates (see Gauthreaux 1980; Baker 1978), is probably complex. It could involve selective factors, such as food supply and climate, and numerous environmental and physiological factors, such as photoperiod, reproductive hormones, and endogenous rhythms. For northern fur seals, learned and innate components are likely to be involved. There are several examples of where learning has been suggested to be involved in migration. When the species leaves the Pribilof Islands for the southern migration, juveniles tend to disperse widely in the North Pacific Ocean, pregnant females tend to travel to the coastal waters off California, and adult males generally remain in the northern Gulf of Alaska (Baker et al. 1970; Fiscus 1978). Baker (1978) has suggested that the juvenile northern fur seals may explore the habitat, and, with age, eventually learn the best wintering areas. Also, an increasing proportion of immature seals return to their natal sites on Pribilof Islands with age (Kenyon and Wilke 1953), although sometimes the natal site is abandoned and a new colony is established, such as at San Miguel Island, CA (Peterson et al. 1968). Baker (1978) has proposed that site recognition may be learned shortly after birth, and with time, the site is usually relocated. However, other components of migration may be innate. For example, the annual timing of arrival for pregnant females on St. Paul Island is remarkably precise. Peterson (1968) calculated the mean arrival date to be 30 June for each of 3 years. Such precision seems unlikely to be the result of only learning. Keyes et al. (1971) examined the pineal gland of this species for seasonal variations in hydroxy-indole levels for various ages of males and females, and postulated photoperiodic regulation of the reproductive cycle.

A physiological event in the lives of young males and females which coincides with the cessation of arriving earlier and returning in greater numbers is the attainment of sexual maturity. Baker (1978) pointed out that sexual maturation controls the initiation of migration in many vertebrates. While a few male northern fur seals begin to produce sperm at 3 yr, most do not do so until about 5 yr (Kenyon et al. 1954; Murphy 1969, 1970). The average female conceives for the first time on her 5th birthday, although typically ovulates for the first time on her 4th (Craig 1964; York 1983). Thus, it was during the years of immaturity that young seals gradually synchronized their arrival schedules with that of the adults. Perhaps the gradual process of gonad maturation in both sexes over several years plays a role in inducing a cohort to migrate progressively earlier in the year and in causing a greater proportion to return to breeding sites.

A relationship between sexual maturity and changes in arrival times on St. Paul Island could explain two other arrival phenomena noted in this study. In the first case, considerable annual varia-

tion was noted in the seasonal pattern of arrival for 4-yr-old males, ranging from the typical pattern seen in 3-yr-olds to that seen in 5-yr-olds. Such differences in the arrival pattern may indicate that the age at which males reach sexual maturity differs between cohorts, a possibility worth further investigation. Variations in the age at sexual maturity could result from annual variations in body growth rate caused in turn by fluctuations in food supply. In the second case, pregnant females at ≥4 yr may have arrived slightly earlier with increasing age. This would take place if the first conception resulted in a later date of parturition than in subsequent years. This is a possibility because, according to Craig (1964), the first ovulation appears to be later than subsequent ovulations. The age of primiparous females spans mainly between 4 and 10 yr (York 1983), and thus the age at first ovulations presumably also spans a similar number of years. Arrival times would tend to be slightly earlier with age from the increased proportion of mature females.

An alternate explanation for seals arriving in progressively larger numbers, may lie in the energetic costs of the return migration from the North Pacific Ocean to the Bering Sea. For yearlings, the energetic costs may be too large for all but a few individuals to return. With age, the relative costs may be more favorable and permit an increased proportion to return.

For each age, males tended to arrive before females. This situation could result if, through selection or learning, the time of the return migration was ultimately established for each sex by the adults. The mechanism controlling the timing of migration in young seals would gradually shift arrival times with age to eventually synchronize with those of the adults. However, because the arrival times of adult males was earlier than that of cows, the arrival times of immature males would also be before those of immature females. The fact that nonpregnant adult females arrived after parous females could be the result of nonpregnant females gaining some advantage in the energetic costs of migration. Since presumably competition exists for food around the Pribilof Islands during the summer, perhaps survival of nonpregnant adult females is enhanced by feeding elsewhere, thus delaying the return migration by 1 mo.

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MODELING LIFE-STAGE-SPECIFIC INSTANTANEOUS MORTALITY RATES, AN APPLICATION TO NORTHERN ANCHOVY, *ENGRAULIS MORDAX*, EGGS AND LARVAE

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ABSTRACT

Life-stage-specific instantaneous mortality rates (IMRs) are often estimated individually for each life stage of an organism using regression analysis. A single estimation procedure for all life stages may be preferable because it would increase the overall precision of the IMRs and also provide a more realistic mortality model. Two such procedures were developed in this paper. One is single-equation model where regression estimates of all IMRs are obtained by fitting a single survivorship function to the entire data set. The other is the maximum likelihood estimator. These models were compared using northern anchovy egg and larval data. The survivorship functions of each were, respectively, exponential and Pareto functions.

The mortality of marine fish can be described by its survival probability $S(t) = P(T > t) = \exp\left[-\int_0^t \lambda(u)du\right]$, where T is the age of the fish and $\lambda(t)$ is the instantaneous mortality rate (IMR) at age t. During their early life history, pelagic marine fishes pass through a series of life stages: eggs, yolk-sac larval, feeding pelagic larval, juvenile and adult stages. The IMR $\lambda(t)$ could be different for some life stages. Therefore, for I life stages, there may be G distinctive IMRs where $G \leq I$. The IMR $\lambda(t)$ is then a piecewise function (Gross and Clark 1975, p. 20-21; Johnson and Kotz 1976, p. 272-273)

$$\lambda(t) = \begin{cases} \lambda_1(t) & 0 \leq t \leq u_1 \\ \lambda_2(t) & u_1 \leq t \leq u_2 \\ \cdot & \cdot \\ \cdot & \cdot \\ \lambda_g(t) & u_{g-1} \leq t \leq u_g \\ \cdot & \cdot \\ \cdot & \cdot \\ \lambda_G(t) & u_{G-1} \leq t \leq u_G \end{cases}$$

where u_g is the maximum age of mortality stanza g. $\lambda_g(t) \neq \lambda_{\dot{g}}(t)$ for $g \neq \dot{g}$. For example, $\lambda_1(t)$ may be the IMR for egg and yolk-sac larval stages, even though each is a different life stage, and $\lambda_2(t)$ the IMR for feeding larvae. As a result, the conditional survival probability, $S_g(t) = P(T > t | T \geq u_{g-1})$ corresponding to $\lambda_g(t)$, will also be different from $S_{\dot{g}}(t)$ and the survival probability $S(t) = (P\ T > t)$ will be

$$S(t) = \begin{cases} S_1(t) & 0 \leq t \leq u_1 \\ S_1(u_1)S_2(t) & u_1 \leq t \leq u_2 \\ \cdot & \cdot \\ \cdot & \cdot \\ \cdot & \cdot \\ \prod_{d=1}^{G-1} S_d(u_d)S_G(t) & u_{G-1} \leq t \leq u_G \end{cases}$$

The common method for estimating $\lambda_g(t)$'s for marine fishes has been to fit $S_g(t)$ to sample age data separately for each life stage or to assume one common $\lambda(t)$ for all life stages and to fit one $S(t)$ to sample data of all life stages (Hewitt and Brewer 1983). For northern anchovy, *Engraulis mordax*, eggs and larvae <20 d old, the IMR $\lambda(t)$ for eggs and yolk-sac larvae is different from that of the feeding larvae (Lo 1985):

$$\lambda(t) = \begin{cases} \lambda_1(t) = \alpha & 0 < t \leq u_1 \\ \lambda_2(t) = \dfrac{\beta}{t} & u_1 \leq t \leq 20 \end{cases} \quad (1)$$

where u_1 is either the hatching time ($t_h \sim 3$ d) or the age of yolk-sac larvae ($t_{ys} \sim 4.5$ d) with the first feeding as the critical period after which mortality decreased. Either t_h or t_{ys} has been used in various models under different assumptions. If morphological differences cause the changes in mortality rates, t_h is a reasonable separation point between

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egg and larval stages. However, predation, the major cause of mortality in the embryonic period, may be similar for eggs and yolk-sac larvae (Hunter[2]). If this is true, then the end of the yolk-sac stage is a reasonable separation point for the mortality stanza.

The conditional survival probability corresponding to IMR in Equation (1) is

$$S_1(t) = e^{-\alpha t} \qquad t \leq u_1 \qquad (2a)$$

and

$$S_2(t) = \left(\frac{t}{u_1}\right)^{-\beta} \qquad u_1 \leq t \leq 20 \qquad (2b)$$

To assess $S_g(t)$ for $g = 1,2$ in Equation (2), anchovy egg and larval data were first divided into K age groups. The mortality curves (Equation (3)) were fitted to the sample mean counts ($\bar{y}_i$) and mean age (t_i) $i = 1,\ldots,K$:

$$E(\bar{y}_i) = \begin{cases} \theta_0\, S_1[t_i;\, \lambda_1(t)] & t_i \leq u_1 \\ \theta_{u_1}\, S_2[t_i;\, \lambda_2(t)] & u_1 \leq t_i \leq 20 \end{cases} \qquad (3)$$

where θ_i is the expected number of fish at age t. Using separate equations like Equation (3) is unsatisfactory for some applications because separate mortality curves may produce discontinuities at transitions between mortality stanzas (or life stages). The purpose of this paper is to obtain a regression estimator and a maximum likelihood estimator (MLE) of the IMRs ($\lambda(t)$). The regression estimator was based upon a single mortality curve for all early life stages of anchovy, and the MLE was based upon a truncated exponential (Equation (2a)) and Pareto (Equation (2b)) likelihood function of time to death (Lo 1985).

In section on Data, I describe the method of anchovy egg and larval data collection and standardization procedures. The standardization procedures are necessary because the gear and sample sizes used to collect eggs differ from those used to collect larvae. In section on Multi-Equation Model, the current estimation procedures for constructing mortality functions for different life stages are presented. In these procedures separate mortality functions are fitted to the data set for each life stage. In the next two sections, I develop two estimation procedures for the IMRs of different life stages from a single analysis: a single mortality function is constructed which is based on the IMRs of different life stages, and the maximum likelihood estimators of life-stage specific IMRs are described. The MLEs of anchovy eggs and larvae (<20 d) are obtained. The results and the comparisons of various models based on anchovy egg and larval data are given in the last two sections.

DATA

The standardized abundance of anchovy eggs and larvae taken in routine biomass surveys was used to elevate different estimation procedures for mortality rates (Smith 1972; Parker 1980). The variables used in the standardization procedures were extrusion through the net, avoidance of the net mouth, and the variation of the water volume filtered per unit depth (Zweifel and Smith 1981).

The northern anchovy spawning area lies off central and southern California and Baja California. The sampling area was divided into 23 regions covering 17.566×10^{11} m^2 (Fig. 1). The central anchovy stock is enclosed by 8 regions (4, 5, 7, 8, 9, 11, 13, and 14) with a total of 5.703×10^{11} m^2 (Duke[3]). In this paper, I study the mortality of egg and larva of central anchovy stock. Anchovy eggs and larvae are sampled by net tows and each tow is a sampling unit. Every year, m_1 egg tows, vertical tows of 0.333 mm mesh with 25 cm diameter mouth opening, and m_2 larval tows using an oblique plankton net of 0.505 mm mesh with 60 cm diameter mouth opening are made. Ages were assigned to life stages using stage specific growth curves (Methot and Hewitt 1980[4]; Lo 1983). The standardized number of larvae in each group was divided by the time that larvae remained at a particular length to yield the sample mean daily larval production per unit area (0.05 m^2). A weighted mean per unit area for the entire survey area (8 regions) was calculated: $\bar{y}_i = \sum_r w_r \bar{y}_{ir}$ where w_r was the weight for region r and $\sum_r w_r = 1$ (Table 1) (Lo 1985) and $\bar{y}_{ir}$ was the sample mean count for i^{th} age group in region r. I considered only larvae smaller than 10 mm (20 d old) because for anchovy larvae larger than 10 mm, the

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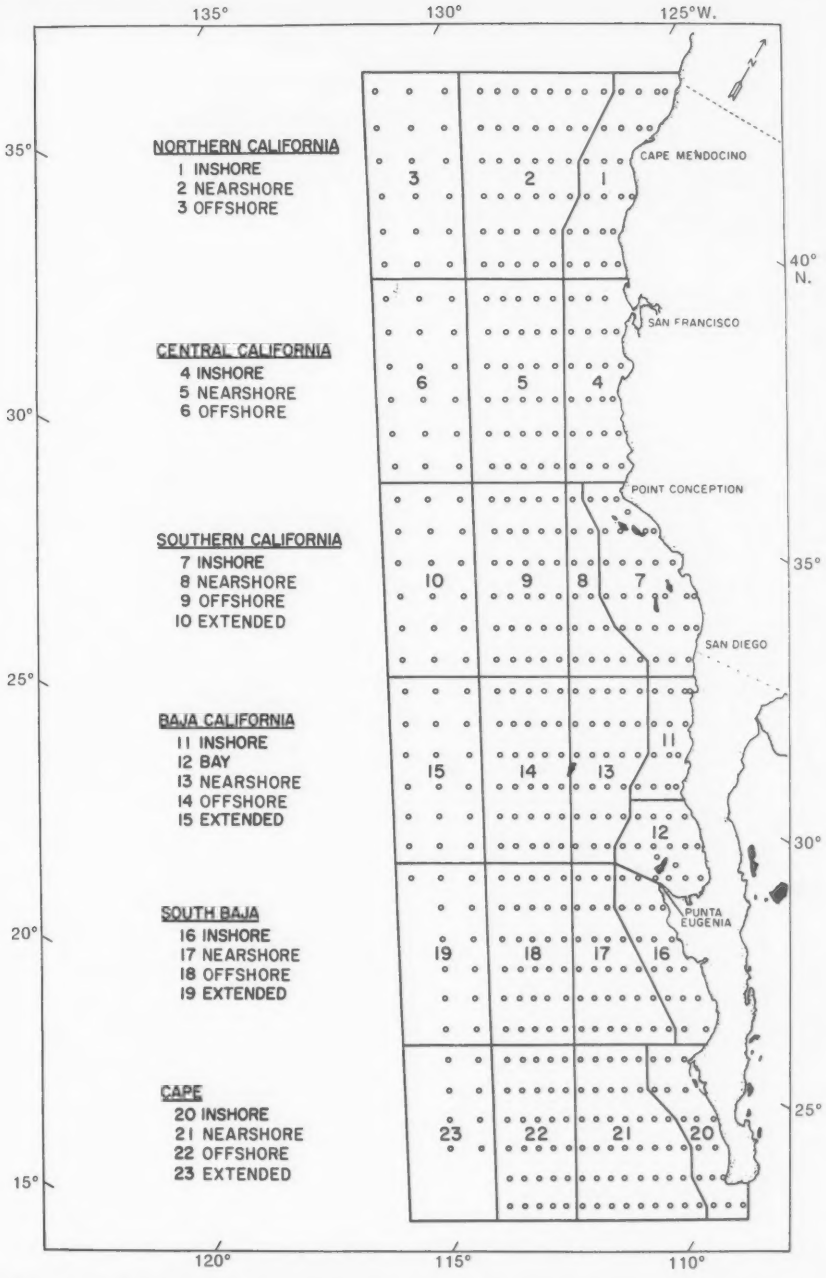

FIGURE 1.—Sampling area for estimating mortality of northern anchovy eggs and larvae (<20 d) with sampling stations denoted by the open circles, and regions denoted by numbers.

TABLE 1.—Group data of anchovy eggs and larvae: Sample mean daily production ($\bar{y}_i$) at age t_i, days for regression estimators and sample mean daily death (n_i) for maximum likelihood estimators (MLEs) of egg and larval mortality.

1980

Regression estimators			MLE			
i	t_i	$\bar{y}_i$	i	t_i	$\bar{y}_i$	[1]n_i
1	0.41666	1.57	1	0.41666	1.57	
2	0.91666	1.21	2	0.91666	1.21	0.36
3	1.41666	1.07	3	1.41666	1.07	0.14
4	1.91666	0.64				
5	2.41666	0.88	4	2.1666	0.76	0.31
6	3.05	0.74	5	3.05	0.74	0.02
7	5.6	0.37	6	5.6	0.31	0.37
8	9.06	0.21	7	9.06	0.21	0.16
9	11.40	0.16	8	11.40	0.16	0.05
10	13.98	0.10	9	13.98	0.10	0.06
11	16.00	0.086	10	16.00	0.086	0.014
12	18.63	0.012	11	18.63	0.072	0.014

1981

Regression estimators			MLE			
i	t_i	$\bar{y}_i$	i	t_i	$\bar{y}_i$	n_i
1	0.41666	1.33				
			1	0.6666	1.665	
2	0.91666	2.00				
			2	1.6666	1.33	0.335
3	1.41666	1.19				
4	1.91666	1.47				
5	2.41666	1.11	3	2.41666	1.11	0.22
6	[2]2.91666	0.60				
			4	3.008	0.915	0.195
7	3.10	1.23				
8	5.98	0.44	5	5.98	0.44	0.475
9	9.45	0.25	6	9.45	0.25	0.19
10	11.97	0.16	7	11.97	0.16	0.09
11	14.37	0.10	8	14.37	0.10	0.06
12	16.53	0.10	9	16.53	0.10	0
13	18.56	0.08	10	18.56	0.08	0.02

1982

Regression estimators			MLE			
i	t_i	$\bar{y}_i$	i	t_i	$\bar{y}_i$	n_i
1	0.41666	0.84				
			1	0.6666	1.21	
2	0.91666	1.57				
3	1.41666	0.76				
			2	1.6666	0.93	0.28
4	1.91666	1.10				
5	2.41666	0.61				
			3	3.42	0.64	0.29
6	4.42	0.67				
7	8.00	0.23	4	8.00	0.23	0.41
8	11.07	0.14	5	11.07	0.14	0.09
9	13.62	0.08	6	13.62	0.08	0.06
10	15.74	0.06	7	15.74	0.06	0.02
11	18.13	0.05	8	18.13	0.05	0.01

1983

Regression estimators			MLE			
i	t_i	$\bar{y}_i$	i	t_i	$\bar{y}_i$	n_i
1	0.41666	1.78	1	0.41666	1.78	
2	0.91666	1.02				
			2	1.1666	1.67	0.11
3	1.41666	2.31				
4	1.91666	0.99	3	1.91666	0.99	0.68
5	2.41666	0.92	4	2.41666	0.92	0.07
6	3.82	0.68	5	3.82	0.68	0.24
7	7.03	0.16	6	7.03	0.16	0.52
8	9.97	0.11	7	9.97	0.11	0.05
9	12.34	0.08	8	12.34	0.08	0.03
10	14.60	0.05	9	14.60	0.05	0.03
11	16.73	0.0405	10	16.73	0.0405	0.01
12	18.88	0.0375	11	18.88	0.0375	0.003

[1]$n_i = \bar{y}_{i-1} - \bar{y}_i$ [2]Used in MLE only.

avoidance of the net becomes a serious bias.

Region	$nm^2 \times 10^{-3}$	$n^2 \times 10^{-10}$	w_r
4	18	6.105	0.107
5	29	9.878	0.174
7	20	6.896	0.119
8	12	4.116	0.072
9	29	9.878	0.174
11	9	3.171	0.054
13	21	7.122	0.125
14	29	9.866	0.174
Total	167	57.031	1.00

The sample mean daily production of eggs and larvae per 0.05 m^2 ($\bar{y}_i$) with its age (t_i) constituted the data base for regression estimates of IMRs of eggs and larvae in MEM and SEM. Mean daily production represent eggs for 0.17 d (4 h) $< t_i \leq$ 3 d, and larvae for 3 d $< t_i \leq$ 20 d; $i = 1, \ldots K$, where K is the total number of age groups. The sample age structure ($\bar{y}_i$, t_i) reflects that of a single cohort under the assumption of steady production over the survey period (Seber 1980). The same data set was also used to generate the sample mean number of eggs or larvae lost per day between two adjacent age groups ($n_i = \bar{y}_{i-1} - \bar{y}_i$). The statistics n_i's were used directly in the MLE. Normally, sample totals were used instead of sample means in MLE. I used n_i's because anchovy eggs and larvae were sampled with different nets and because the number of egg tows was different from that of larvae.

MULTI-EQUATION MODEL (MEM)

In the current estimation procedures, separate mortality curves are constructed (Equation (3)) for

the IMRs ($\lambda(t)$) of anchovy eggs and larvae. If the life-stage-specific IMR is the main objective, the MEM is an easy method for obtaining the estimates of IMRs. The mortality curves (Equation (3)) are nonlinear functions of age (t). The IMRs can be estimated by either nonlinear regression (NR) or linear regression (LR) after the data set ($\bar{y}_i$, t_i) is transformed. The NR is based upon the assumption that the errors are additive. The observed mean daily production ($\bar{y}_i$) relates to the conditional survival probability as

$$\bar{y}_i = \theta_0 S_1[t_i; \lambda_1(t)] + e_{1i}$$

$$= \bar{y}_0 e^{-\alpha t_i} + e_{1i} \qquad t_i \leq u_1 \qquad (4a)$$

$$\bar{y}_i = \theta_{u_1} S_1[t_i; \lambda_2(t)] + e_{2i}$$

$$= \bar{y}_{u_1}\left(\frac{t}{u_1}\right)^{-\beta} + e_{2i} \qquad u_1 \leq t_i \leq 20 \qquad (4b)$$

where $u_1 = t_h \sim 3$ d old. Nonlinear regression estimation procedures provided by standard statistical packages such as BMDP statistical software (Dixon et al. 1983) are then used to estimate the parameters of IMRs, i.e., α and β.

The LR assumes that the errors are multiplicative. The observed daily production ($\bar{y}_i$) relates to the conditional survival probability in the form of

$$\bar{y}_i = \theta_{u_{g-1}} S_g(t_i; \lambda_g(t))\, e_{gi} \qquad \text{for } g = 1,2.$$

The logarithm of both sides of the equation yields two linear functions

$$\ln(\bar{y}_i) = A - \alpha t_i + \in_{1i} \qquad t_i \leq u_1 \qquad (5a)$$

$$\ln(\bar{y}_i) = B - \beta \ln\left(\frac{t_i}{u_1}\right) + \in_{2i} \qquad u_1 \leq t_i \leq 20. \qquad (5b)$$

Equation (5a) is then fitted to data set ($\ln(\bar{y}_i)$, t_i for $t_i \leq u_1$), and Equation (5b) is fitted to data set ($\ln(\bar{y}_i)$, $\ln(t_i/u_1)$ for $u_1 \leq t_i \leq 20$ d) to estimate α and β.

SINGLE-EQUATION MODEL (SEM)

The SEM consolidates all the conditional survival probabilities ($S_g(t)$) from each mortality stanza into a single equation. It not only eliminates discontinuities at transitions between life stages, but also improves the precision of overall mortality estimates because of the large sample size. Moreover, the SEM makes it possible to estimate the IMR for life stages where data are scarce.

Based upon Equation (2), $S(t_i)$ of anchovy eggs and larvae is

$$S(t_i) = \begin{cases} S_1(t_i) & t_i \leq u_1 \\ S_1(u_1)S_2(t_i) & u_1 \leq t_i \leq 20 \end{cases}$$

or

$$S(t_i) = \begin{cases} S_1(t_i)S_2(u_1) & t_i \leq u_1 \\ S_1(u_1)S_2(t_i) & u_1 \leq t_i \leq 20 \end{cases}$$

where $S_1(u_1) = P(T > u_1 | T \geq 0) = e^{-\alpha u_1}$, $S_2(u_1) = P(T > u_1 | T \geq u_1) = 1$, and $u_1 = t_{ys} = 4.5$ d. Thus by creating two new independent variables x_{1i} and x_{2i} such that

$$x_{1i} = \begin{cases} t_i & t_i \leq u_1 \\ u_1 & u_1 \leq t_i \leq 20 \end{cases}$$

and

$$x_{2i} = \begin{cases} u_1 & t_i \leq u_1 \\ t_i & u_1 \leq t_i \leq 20 \end{cases}$$

it follows that $S(t_i) = S_1(x_{1i})S_2(x_{2i})$ and the mortality curve can be written as

$$E(\bar{y}_i) = \theta_0 S_1(x_{1i})S_2(x_{2i}) = \theta_0 e^{-\alpha x_{1i}}\left(\frac{x_{2i}}{u_1}\right)^{-\beta}. \qquad (6)$$

The data set for fitting Equation (6) looks like

age group (i)	*age* (t_i)	$\bar{y}_i$	x_{1i}	x_{2i}	
1	t_1	$\bar{y}_1$	t_1	u_1	
2	t_2	$\bar{y}_2$	t_2	u_1	
.	.	.	.	.	
.	.	.	.	.	
.	.	.	.	.	
i	t_i	$\bar{y}_i$	$\bar{u}_1$	t_i	$u_1 = 4.5$ d
.	.	.	.	.	
.	.	.	.	.	
k	t_k	$\bar{y}_k$	$\bar{u}_1$	t_k	

In order to use Equation (6) to estimate the IMRs of eggs and larvae in Equation (1), a combined data

set ($\bar{y}_1$, x_{1i}, x_{2i}), which includes all the data from each life stage and the maximum ages of mortality stanzas (u_g's), is important to ensure the accuracy of the estimates of the IMRs. The determination of u_g's depends primarily on the changes of the mortality rates, which may be related to the changes in morphology or behavior that affects mortality rates. In the best fit of the SEM, however, the end points of morphological patterns may not correspond to the maximum ages. Three life stages were identified for anchovy eggs and larvae, with the end point of mortality stanza 1 being the average age of yolk-sac larvae (u_1 = 4.5 d). In the MEM, the hatching time (t_h) was used, but, the best fit of the SEM occurred when u_1 = 4.5 d. Two mortality stanzas were assigned to three life stages of anchovy (<20 d) because from the existing data, no evidence for a change in the IMRs within a life stage existed although the data may not have been adequate to detect such changes.

The regression estimates of the IMRs for the SEM can be obtained by either NR or LR as described in the previous section. If NR is used, Equation (6) is fitted to the data set ($\bar{y}_i$, x_{1i}, and x_{2i}) directly to obtain estimates of parameters of $\lambda_1(t)$ and $\lambda_2(t)$. Because the variance of egg data is larger than that of larvae, a weighted NR (WNR) would be preferable. If errors are assumed to be multiplicative, taking the logarithm of both sides of the Equation (6) yields

$$\ln(\bar{y}_i) = A - \alpha x_{1i} - \beta \ln\left(\frac{x_{2i}}{u_1}\right) + \in_i. \qquad (7)$$

The data set ($\ln(\bar{y}_i)$, x_{1i}, and $\ln(x_{2i}/u_1)$) is then used to estimate α and β through linear least squares regression.

MAXIMUM LIKELIHOOD ESTIMATOR (MLE)

The MLE is presented here as an alternative method of estimating IMRs. Because the data used for mortality estimators are grouped by age, I followed the procedures described by Kulldorff (1961) and McDonald and Ransom (1979) for grouped data. Here, $N_i = Y_{i-1} - Y_i$ (number of deaths between ages t_{i-1} and t_i) of a single cohort are multinomial variables, each with probability

$$P_i = S(t_{i-1}) - S(t_i).$$

The likelihood function of N_i's for the whole life cycle ($i = 1, \ldots, I$, and $Y_I = 0$) is

$$L(N_i, P_i(z'); i = 1, \ldots, I) \propto \prod_{i=1}^{I} P_i(z')^{N_i}$$

$$= \prod_{i=1}^{I} [S(t_{i-1}) - S(t_i)]^{N_i} \qquad (8)$$

where z is the parameter vector in $\lambda(t)$. The derivatives of the logarithm of likelihood function with respect to the parameters z's are set equal to zero. Solutions to the simultaneous equations

$$\frac{\partial \ln L}{\partial z_i} = 0$$

are MLEs of z, if certain conditions are satisfied (Kulldorff 1961). In marine fish only the IMRs of a few life stages are considered because of the lack of data. It is then necessary to compute the conditional probability

$$P_i = P(t_{i-1} \leqslant T < t_i \mid T \in D)$$

$$= [S(t_{i-1}) - S(t_i)]/P(T \in D)$$

where D is the domain of ages of life stages considered.

Because I considered only the IMRs of anchovy eggs and larvae of ages >4 h (0.17 d) and <20 d, the conditional probabilities are computed from a truncated exponential and Pareto survival probability (Equation (2)) (Gross and Clark 1975, p. 128-132):

$$P_i = P(t_{i-1} < T \leqslant t_i \mid t_1 < T \leqslant 20)$$

$$= (S(t_{i-1}) - S(t_i))/(S(t_1) - S(20))$$

$$P_i = \begin{cases} \dfrac{e^{-\alpha t_{i-1}} - e^{-\alpha t_i}}{e^{-\alpha t_1} - e^{-\alpha u_1}\left(\dfrac{20}{u_1}\right)^{-\beta}} & t_i \leqslant u_1 \\ \dfrac{e^{-\alpha u_1}\left[\left(\dfrac{t_{i-1}}{u_1}\right)^{-\beta} - \left(\dfrac{t_i}{u_1}\right)^{-\beta}\right]}{e^{-\alpha t_1} - e^{-\alpha u_1}\left(\dfrac{20}{u_1}\right)^{-\beta}} & u_1 \leqslant t_i \leqslant 20. \end{cases} \qquad (9)$$

Then the likelihood function of N_i's for anchovy eggs and larvae of ages <20 d is

$$L \propto \prod_{i=2}^{k} P_i^{N_i} = \left[\prod_{i=2}^{k} (S(t_{i-1}) - S(t_i))^{N_i} \right] / \left[S(t_1) - S(20) \right]^{\sum_{i=2}^{k} N_i}$$

and

$$\ln(L) = \sum_{i=2}^{k} [N_i \ln(P_i)] = \sum_{i=2}^{c} [N_i \ln(P_i)] + \sum_{i=c+1}^{k} [N_i \ln(P_i)] \tag{10}$$

where $N_i = m(\bar{y}_{i-1} - \bar{y}_i) = m \cdot n_i$ and c is max(i) for $t_i \leqslant 3$ d (u_1). Substituting Equation (9) for P_i in Equation (10) yields

$$\ln(L) = \sum_{i=2}^{c} N_i \ln\left(e^{-\alpha t_{i-1}} - e^{-\alpha t_i}\right) + \sum_{c+1}^{k} \left[N_i(-\alpha u_1 + \beta \ln u_1) + N_i \ln(t_{i-1}^{-\beta} - t_i^{-\beta}) \right]$$

$$- \sum_{i=2}^{k} N_i \ln\left[e^{-\alpha t_1} - e^{-\alpha u_1} \left(\frac{20}{u_1}\right)^{-\beta} \right]. \tag{11}$$

Solving simultaneous equations $\dfrac{\partial \ln L}{\partial \alpha} = 0$ and $\dfrac{\partial \ln L}{\partial <}$ for α and β gives their MLEs.

The asymptotic variance-covariance (ASVAR-COV) of MLEs of α and β was computed according to Kulldorff (1961, p. 86-87):

$$\begin{bmatrix} \text{As var}(\alpha) & \\ \text{As cov}(\alpha,\beta) & \text{As var}(\beta) \end{bmatrix}\Bigg|_{\hat{\alpha},\hat{\beta}} = (1/N) \begin{bmatrix} a_{11} & \\ a_{21} & a_{22} \end{bmatrix}\Bigg|_{\hat{\alpha},\hat{\beta}} = (1/N)\, A_{\hat{\alpha},\hat{\beta}}$$

$$= -\frac{1}{N} \begin{bmatrix} \sum_{i=2}^{k} P_i \dfrac{\partial^2 \ln P_i}{\partial \alpha^2} & \\ \sum_{i=2}^{k} P_i \dfrac{\partial^2 \ln P_i}{\partial \alpha \partial \beta} & \sum_{i=2}^{k} P_i \dfrac{\partial^2 \ln P_i}{\partial \beta^2} \end{bmatrix}^{-1}\Bigg|_{\hat{\alpha},\hat{\beta}} \tag{12}$$

For detailed derivation of the MLEs, see the Appendix.

Conceptually, abundance declines monotonically with increasing age, but this may not occur in the sample. Although its absence does not complicate regression analysis, corrections are required when the MLEs are used. The MLEs are functions of sample totals $N_i = (\bar{y}_{i-1} - \bar{y}_i)m$, $N_i \geqslant 0$, and can also be expressed as function of sample proportions N_i/N (Equations (A1) and (A2)), which are equal to the ratios of differences of sample mean daily productions $(\bar{y}_{i-1} - \bar{y}_i)/(\bar{y}_1 - \bar{y}_k) = n_i/n$ (see Appendix). The quantity $n_i = N_i/m$ is the sample mean daily death between two adjacent groups. The MLEs require $N_i \geqslant 0$. Due to sampling error, it is possible to observe more individuals in the older group than the adjacent younger group, i.e., $\bar{y}_{i-1} < \bar{y}_i$. If so, some adjacent groups

$(\bar{y}_i, t_i)$ have to be combined so that $\bar{y}_i > \bar{y}_{i'}$ for $t_i < t_{i'}$. The ratio n_i/n can be used in place of N_i/N to compute the MLEs. This correction is inappropriate if the reason for $\bar{y}_i > \bar{y}_{i'}$, for $t_i < t_{i'}$ is that individuals were evicted from the sampling area or immigrated into it, as such movements violate the assumption of a stationary population.

Although n_i's are sufficient for computing point estimates of the MLE, the total number of deaths between ages t_1 and t_k ($N = m(\bar{y}_1 - \bar{y}_k)$ is required for computation of the ASVAR-COV of the MLEs. N can then be used to determine minimum number of tows (m_1) for the youngest stage through $m_1\bar{y}_1 \doteq N$ for a given precision of the MLE. Although the sample size for eggs may differ from that of larvae, an equal number of sample sizes is assumed to compute the ASVAR-COV. The minimum number of egg tows can be determined by $m_1 = N/\bar{y}_1$.

RESULTS

Both the MEM and the SEM were fitted to the basic data ($\bar{y}_i$, t_i; 0.17 d $< t_i \leq$ 20 d) collected from 1980 to 1983, using NR and LR (Table 1, Fig. 2). The point estimates and their asymptotic standard errors are listed in Table 2 and Figure 3. NR and LR produced similar estimates of the IMRs for the MEM. When the SEM was applied to the combined egg and larval data, the WNR was also used to compute the IMRs in addition to NR and LR because of the inequality of the variances among life stages. The variance of egg counts was higher than that of larvae because eggs were more patchily distributed than larvae. Because of this, the inverse of the variances of sample means of eggs and larvae was used as the weights for the WNR. The estimates from the WNR were similar to those from LR and the standard errors from both methods were lower than those from NR.

The WNR estimates of egg IMRs from the SEM were more precise than estimates from the MEM, whereas the most precise estimates of larval IMRs were provided by the MEM using NR. The SEM was more precise than the MEM for eggs but not for the larvae, because the variance of eggs was larger than that of larvae. Thus, when eggs and larvae were combined in an SEM, the variance around the single equation was smaller for the eggs and larger for the larvae. Nevertheless, the SEM produced larval IMRs with reasonable precision when the WNR was used. Therefore, the SEM WNR is suitable for ap-

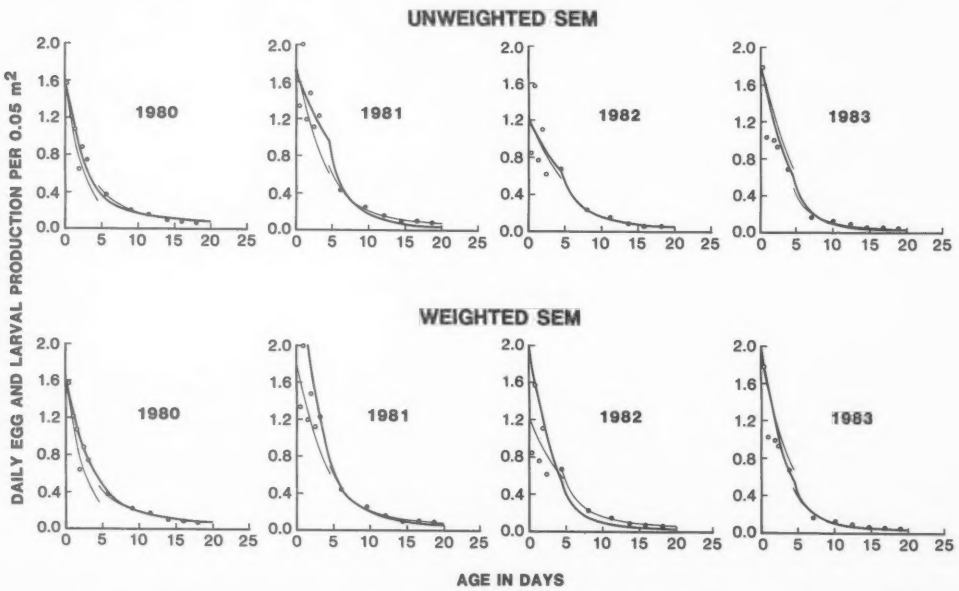

FIGURE 2.—Observed daily anchovy egg and larval production/0.05 m² (○ = eggs, ● = larvae), and the mortality curves from the MEM (two short curves) and the SEM (one single curve) using unweighted and weighted nonlinear regression for 1980-83 field collected data.

TABLE 2.—Estimates from multi-equation model (MEM), single-equation model (SEM), and maximum likelihood estimator (MLE) for anchovy egg and larval mortality ($\hat{\alpha}$ and $\hat{\beta}$), and their standard error (SE) based upon 1980-83 field data where K is number of age groups and m is number of tows used in each model. For both MEM and SEM, nonlinear regression (NR), linear regression (LR) and weighted nonlinear regression (WNR) estimates are given.

	Egg mortality			Larval mortality		
	$\hat{\alpha}$	SE	$K(m)$	$\hat{\beta}$	SE	$K(m)$
1980						
MEM						
NR	0.39	0.103	5(961)	1.22	0.0314	7(199)
LR	0.35	0.13		1.32	0.06	
SEM						
NR	0.32	0.05	12(1,160)	1.06	0.41	12(1,160)
WNR	0.25	0.02		1.33	0.06	
LR	0.24	0.05		1.36	0.13	
MLE	0.36	0.012	11(961)	1.28	0.09	11(961)
		0.016	(500)		0.12	(500)
		0.02	(300)		0.16	(300)
		0.03	(199)		0.27	(199)
1981						
MEM						
NR	0.13	0.16	5(1,134)	1.53	0.032	7(403)
LR	0.13	0.15		1.54	0.06	
SEM						
NR	0.13	0.07	12(1,537)	2.19	0.96	12(1,537)
WNR	0.33	0.06		1.70	0.18	
LR	0.20	0.05		1.64	0.15	
MLE	0.24	0.008	10(1,134)	0.96	0.06	10(961)
		0.01	(500)		0.08	(500)
		0.02	(300)		0.11	(300)
		0.01	(403)		0.10	(403)
1982						
MEM						
NR	0.17	0.26	5(992)	1.81	0.036	6(96)
LR	0.19	0.24		1.87	0.065	
SEM						
NR	0.14	0.10	11(1,088)	1.77	1.46	11(1,088)
WNR	0.13	0.04		1.83	0.36	
LR	0.12	0.07		1.85	0.20	
MLE	0.24	0.008	8(992)	1.20	0.08	8(992)
		0.01	(500)		0.11	(500)
		0.015	(300)		0.14	(300)
		0.03	(100)		0.25	(100)
1983						
MEM						
NR	0.23	0.29	5(850)	2.05	0.11	7(78)
LR	0.27	0.25		1.80	0.10	
SEM						
NR	0.26	0.19	12(928)	2.45	2.71	12(928)
WNR	0.30	0.05		2.23	0.28	
LR	0.33	0.08		1.84	0.22	
MLE	0.32	0.007	11(850)	2.48	0.10	11(850)
		0.01	(500)		0.14	(500)
		0.013	(300)		0.18	(300)
		0.02	(80)		0.35	(80)

plications where it is preferable to estimate IMRs for egg and larvae simultaneously (e.g., simulation studies of mortality at all life stages). The SEM is preferable for modeling the mortality curves through all life stages because it eliminates the multiple estimates that occur at the endpoint of each life stage (Fig. 2). In addition, the SEM allows estimation of the IMRs for all life stages even when data for some life stages are inadequate for independent estimation of a life-stage-specific IMR. In comparing NR and LR, the estimates of IMRs from these two procedures were similar, despite the different assumptions about the error term. One complication of using LR is that the abundance for any

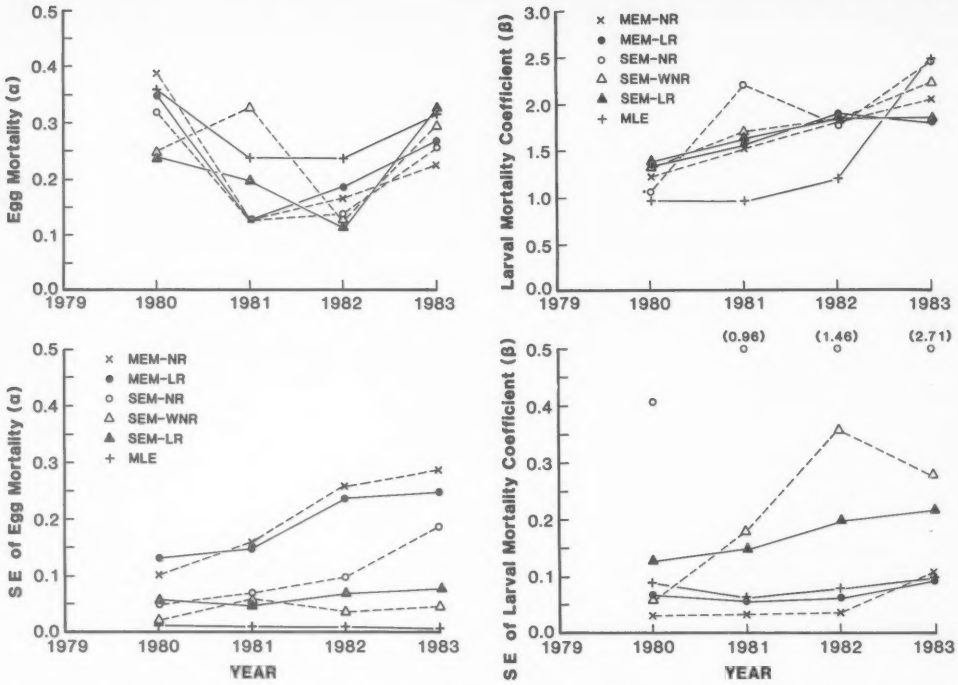

FIGURE 3.—Estimated anchovy egg mortality ($\hat{\alpha}$), larval mortality coefficient ($\hat{\beta}$), and their standard error (SE) using multi-equation model (MEM), single-equation model (SEM), and maximum likelihood estimator (MLE) for 1980-83.

specific age needs to be transformed back to the original unit. Direct inverse transformation may bias the estimates. Thus, the LR may not be appropriate for biomass estimation or other applications where a transformation back to original units is required.

In addition to the above regression models, the MLEs of egg and larval IMRs were also computed based on the data set $n_i = \bar{y}_{i-1} - \bar{y}_i$, $i = 1, \ldots k$ (Equations (A1) and (A2), Table 1). The ASCOVVAR for anchovy egg and larval mortality rates requires the total number of eggs and larvae that died between ages 4 h and 20 d from the sample (N). It is not possible to obtain N directly from $m\bar{y}_1$ (i.e. $N \doteq m\bar{y}_1$) because eggs and larvae are sampled with different nets and in different regions. Anchovy eggs have a more concentrated and patchy distribution than larvae which are less numerous and distributed more uniformly throughout the entire survey area because of the diffusion of larvae after hatching (Hewitt 1982). Zero density of eggs was assumed for the offshore regions where eggs were not sampled to compute the weighted average egg production $\bar{y}_i = \sum_r w_r \bar{y}_{ir}$. I then divided $m_1\bar{y}_1$ by the proportion of area sampled ($q = \sum_r w_r$ where w_r's are summed over the regions where egg tows were taken) to obtain sample daily death N in $[t_1, t_k)$. Thus, $N = m_1\bar{y}_1/q$; q ranges from 0.53 to 0.82 for 1980-83. Four sets of sample sizes were considered: $m = m_1$, 500, 300, m_2 where m_1 is the actual number of egg tows and m_2, actual number of larval tows (Table 2). For any given N, one obtains the ASVAR-COV of α and β by dividing a_{ij} by N where a_{ij}'s are the elements in matrix A of Equation (12).

The MLE point estimates $\hat{\alpha}$ and $\hat{\beta}$, were between the estimates yielded by the SEM and the MEM in most cases. The precision of the MLE for egg IMR was higher than that of the regression estimates. The standard error of the MLE of the larval IMR was between those of the MEM and SEM regression estimates (Table 2, Fig. 3).

DISCUSSION

All the estimates of instantaneous mortality rates (IMR) discussed in this paper were computed from age (stage) frequency data. To ensure the unbiasedness of the estimates, three assumptions have to be met: a stationary population, reliable growth curves, and accurate samplers. Any violation of these assumptions will cause biases in the mortality estimates. Nets usually do not retain fish of all sizes because some small fish extrude through the net and some large fish avoid the net. Thus the estimates of size-specific retention rates are essential correction factors for the catch. If fish migrate at a significant rate, either the migration rate should be estimated or the sampling area should be expanded to eliminate migration problems, for migration violates the assumption of a stationary population and thus biases the mortality. Because growth curves are normally used to assign age to stage of eggs and larvae, biased growth curves would lead to inaccurate age assignments which definitely would bias the mortality estimates.

Although modeling the mortality rates of the early life stages of anchovy is the focus of this paper, I have shown that the SEM (Fig. 2) can be applied to any continuous process whose parameters are life-stage specific and generally estimated separately. For example, many allometric relations such as the growth curves may have different instantaneous growth rates for different life stages. A single continuous growth curve for the whole life cycle is possible using the SEM which allows greater latitude of modeling life-stage-specific growth rates than modeling the instantaneous growth rate for the whole life cycle as proposed by Schnute (1981). However, the SEM does require knowledge of the forms of instantaneous rates and the endpoint of each mortality stanza (or life stage).

In this study, the determination of a cutoff point between life stages was based upon examination of the empirical data and biological implications. It is conceivable to include the cutoff point (u_1) as one of the parameters in both SEM and MLE (Matthews and Farewell 1982). The cutoff point can then be estimated directly through the models. Matthews and Farewell considered the exponential mortality curve with one cutoff point and obtained MLE of the cutoff point (change point). For anchovy egg and larvae, the cuttoff point for the eggs and larvae up to 20 d old was easily determined from the IMR and age data (Lo 1985). Estimation of the cutoff point through SEM or MLE would be laborious and any improvement may be minimal. However, the estimates through the models would eliminate the problem of whether u_1 should be hatching time or the age of yolk-sac larvae.

Comparison of these two regression models with the MLEs based on anchovy egg and larval data indicated that the point estimates of the IMRs were similar. The SEM using WNR provided the most precise egg IMR which was nearly the same as the MLE. The MEM, using NR, provided the most precise estimates of larval IMR's. The regression estimators of the IMR's are easier to compute than the MLEs, yet they require larger sample sizes than the MLEs. If money is not a constraint, the SEM is preferred to the MLE. Otherwise, the MLE should be used. Based upon 1980 anchovy egg and larval data, 300 tows for eggs and larvae each (a total of 600 tows) could guarantee MLEs of α and β with cv = 0.10. The current sampling design (egg tows $\sim$ 1,000) seems to use an excessive number of egg tows for the MLEs of egg and larval IMRs. If the larval IMR is the only parameter to be estimated, the MEM is recommended.

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APPENDIX

The two partial deviations of $\ln L$ (Equation (11)) are

$$\frac{\partial \ln L}{\partial \alpha} = N \sum_{i=2}^{c} \frac{N_i}{N}\left[\frac{-t_{i-1} - t_i e^{-\alpha\Delta_i}}{1 - e^{-\alpha\Delta_i}}\right] - u_1 \sum_{i=c+1}^{k} \frac{N_i}{N} + t_1 - (u_1 - t_1)\left[e^{\alpha(u_1 - t_1)}\left(\frac{20}{u_1}\right)^{\beta} - 1\right]^{-1} = 0 \quad \text{(A1)}$$

$$\frac{\partial \ln L}{\partial \beta} = N \sum_{i=c+1}^{k} \frac{N_i}{N}\left[\ln u_1 + \frac{-\ln t_{i-1} + \left(\frac{t_i}{t_{i-1}}\right)^{-\beta} \ln t_i}{1 - \left(\frac{t_i}{t_{i-1}}\right)^{-\beta}}\right] - \ln\left(\frac{20}{u_1}\right)\left[e^{\alpha(u_1 - t_1)}\left(\frac{20}{u_1}\right)^{\beta} - 1\right]^{-1} = 0 \quad \text{(A2)}$$

where $\Delta_i = t_i - t_{i-1}$ and $u_1 \sim 3$.

Both Equations (A1) and (A2) depend on the proportion N_i/N rather than the absolute counts (N_i's). In order to have a unique solution of α and β, it is necessary to have

$$\frac{\partial^2 \ln L}{\partial \alpha^2} < 0 \quad \text{and} \quad \frac{\partial^2 \ln L}{\partial \beta^2} < 0. \quad \text{(A3)}$$

Moreover, the conditions

$$\lim_{\alpha \to 0} \frac{\partial \ln L}{\partial \alpha} > 0, \quad \lim_{\alpha \to \infty} \frac{\partial \ln L}{\partial \alpha} < 0$$

and (A4)

$$\lim_{\beta \to 0} \frac{\partial \ln L}{\partial \beta} > 0, \quad \lim_{\beta \to \infty} \frac{\partial \ln L}{\partial \beta} < 0$$

guarantee a positive solution of α and β. Equation (A3) leads to the following constraints

$$1 < \frac{\left[e^{\alpha(u_1 - t_1)}\left(\frac{20}{u_1}\right)^{\beta} - 1\right]^2}{(u_1 - t_1)^2\left(\frac{20}{u_1}\right)^{\beta} e^{(u_1 - t_1)\alpha}} \sum_{i=2}^{c} \frac{N_i}{N}\left(\frac{t_i - t_{i-1}}{1 - e^{-\alpha(t_i - t_{i-1})}}\right)^2 e^{-\alpha(t_i - t_{i-1})} \tag{A5}$$

and

$$1 < \frac{\left[e^{\alpha(u_1 - t_1)}\left(\frac{20}{u_1}\right)^{\beta} - 1\right]^2}{\left[\ln\left(\frac{20}{u_1}\right)\right]^2\left(\frac{20}{u_1}\right)^{\beta} e^{\alpha(u_1 - t_1)}} \sum_{i=c+1}^{k} \frac{N_i}{N} \frac{\left(\frac{t_i}{t_{i-1}}\right)^{-\beta}\left[\ln\frac{t_i}{t_{i-1}}\right]^2}{\left[1 - \left(\frac{t_i}{t_{i-1}}\right)^{-\beta}\right]^2}. \tag{A6}$$

After algebraic manipulation, it was easy to see that Equation (A4) was true for this truncated exponential and the Pareto MLE. We used an iterative procedure to select the MLE of α and β, which satisfies not only Equation (A3) but also the constraints of Equations (A5) and (A6).

The partial derivations in each entry of matrix A (Equation (12)) are

$$\frac{\partial^2 \ln P_i}{\partial \alpha^2} = -\left(\frac{\Delta_i}{e^{\alpha\Delta_i} - 1}\right)^2 e^{\alpha\Delta_i} + (u_1 - t_1)^2 \frac{\left(\frac{20}{u_1}\right)^{\beta} e^{\alpha(u_1 - t_1)}}{\left[e^{\alpha(u_1 - t_1)}\left(\frac{20}{u_1}\right)^{\beta} - 1\right]^2}$$

$$\frac{\partial^2 \ln P_i}{\partial \beta^2} = \frac{\left[\ln\left(\frac{20}{u_1}\right)\right]^2\left(\frac{20}{u_1}\right)^{\beta} e^{\alpha(u_1 - t_1)}}{\left[e^{\alpha(u_1 - t_1)}\left(\frac{20}{u_1}\right)^{\beta} - 1\right]^2}$$

and

$$\frac{\partial^2 \ln P_i}{\partial \alpha \partial \beta} = \frac{(u_1 - t_1)\left(\frac{20}{u_1}\right)^{\beta} e^{\alpha(u_1 - t_1)} \ln\left(\frac{20}{u_1}\right)}{\left[e^{\alpha(u_1 - t_1)}\left(\frac{20}{u_1}\right)^{\beta} - 1\right]^2}.$$

METHODOLOGICAL PROBLEMS IN SAMPLING COMMERCIAL ROCKFISH LANDINGS

A. R. SEN[1]

ABSTRACT

The present sample survey plan, for the estimation of age and species composition of California rockfish landings, which is stratified two-stage with port-month group as a stratum, poses serious operational problems in data collection. A revised plan is suggested which is workable. Formulas have been developed for estimating total catch and its error by species-sex-age groups; optimum sampling and subsampling fractions have been obtained for a given cost function and the precision of the estimator is compared with two other estimators. The method developed has been extended to cover situations other than rockfish.

The paper also deals with double-sampling for specified cost for the estimation of age composition of a species, which is important to predict the status of a stock in future years, the inherent problems in data collection in commercial fisheries, and the measurement errors involved in the survey.

Estimates of the total catch (in terms of number) by species-sex-age and by area of landing and during a given time for commercial rockfish caught in California north of point Arguello are currently based on a probability sample of landings. The commercially important species of rockfish taken by California's fishery with mixed species are widow rockfish, *Sebastes entomelas*; bocaccio, *Sebastes paucispinis*; and chilipepper, *Sebastes goodei*.

A study was undertaken during 1983 under agreement between the present author, the Humboldt State University Foundation, and the Tiburon Laboratory of the National Marine Fisheries Service, NOAA, to determine if the present sampling plan for the estimation of species and age-composition of California rockfish landings is workable. The study revealed that the current plan is not operationally feasible. A revised plan is proposed which is workable and would provide efficient estimates of the parameters based on existing catch data within the usual limitations of budget and personnel and under the assumptions made in the plan. Formulas have been developed for the ratio estimators of mean and total catch and their errors. Optimum sampling and subsampling fractions have been obtained for a given cost function and the precision of the estimator is compared with two other estimators.

For most theoretical population work and for management purposes, the knowledge of the age composition is important to predict the status of the stock in future years. Fridricksson (1934) developed the age-length key method for determing age composition from a large number of length measurements. Fridricksson's approach was improved by Ketchen (1950) who provided more accurate results for age groups at the extremities of the distribution. Kutkuhn (1963) mentioned the limitations of the age-length key approach except in situations where price differentials may demand sorting of landings by size criterion. Westrheim and Ricker (1978) pointed out that the age-length key approach will almost always give biased estimates. Clark (1981) and more recently Bartoo and Parker (1983) dealt with methods for control or elimination of bias. Following the method of Tanaka (1953) in which stratification occurs after subsampling for age, Kutkuhn (1963) estimated absolute age composition of California salmon landings by port-month groups. He showed that the sampling procedure is not effective unless the age sample is at least five times costlier than the length sample.

Mackett (1963) found double sampling more efficient than simple random sampling with fixed sampling costs for estimating relative age composition of Pacific albacore landings.

Southward (1976) found that a sample of otoliths proportional to the length frequency of sampled fish from each port was preferable to fixed sample size procedure for estimating age composition of Pacific halibut. Kimura (1977) arrived at the same conclusion as Southward by following a somewhat different approach.

We will present some of the important considera-

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tions in sampling for estimating age composition of rockfish landings based on recent widow rockfish data from the California coast. Finally, we will describe some of the measurement errors, which would normally occur in simple random sample of individual fish and which are taken care of in cluster sampling adopted in our approach.

The sampling plan arrived at may produce usable results under the assumptions stated, though some of the assumptions have been under attack during recent years.

DESIGN OF THE SURVEY

Rockfish are being landed at 14 points on the California coast. Of these, three cater only to commercial fishing, four to sport fishing, and seven to both sport and commercial fishing. The 10 commercial ports are grouped into 6 port groups with a sampler (six in all) assigned to each of the 6 ports—Eureka, Fort Bragg, Bodega Bay, San Francisco, Monterey, and Morro Bay.

The commercial trawlers make trips varying in length from 1 to 8 d. These vessels maintain log books to keep records of area fished and appropriate catch for each tow. Sampling by tow is generally not feasible because it is not possible for the sampler to be on board during haul time. For the same reasons no estimates of fish being rejected and returned to the sea are obtained because this would involve collection of discarded fish from randomly selected tows within sampled trips.

Selection Procedure

A two-stage stratified random sampling plan was adopted with port-month group as a stratum and boat trips within a stratum as first-stage sampling units. Fish are sorted at sea into market categories. The first stage sampling units are poststratified into categories and at least one cluster of a given weight is subsampled within each sort-type from a first-stage sampling unit. Categories are based upon species composition, size, and quality, but in other contexts they could be strictly size or species categories. Cluster (box) of 25 lb is taken when sampling small fish, or any time small rockfish are landed such that there would be more than 20 fish in the 50-lb cluster. In all other cases 50-lb standard cluster size is selected. A cluster is next separated by number of each species and its weight, which are recorded along with sex, total length, and otolith of each member of a species in the cluster.

The instructions are to "sample all market categories (sorts) from a boat, and from as many boats as possible and select:

"(i) 1 cluster per 20,000 lb of widow rockfish landed by each boat, up to 4 clusters,
"(ii) 1 cluster for all other species, if less than 5,000 lb landed, and
"(iii) 2 clusters for all species if more than 5,000 lb are landed.

"The second cluster should not be taken if this precludes sampling another boat."

Estimation with Poststratification of Sample Trips by Categories

Consider the problem of estimation of total catch of a given species for a port-month stratum. Equations for estimation of other characteristics for fisheries with mixed species are straightforward and can be obtained by substituting the value of the characteristic for the catch of the species. Totals across strata are formed by simple additon.

Notation

For a given species, let

N = total number of trips,
n = number of randomly sampled trips,
W = total weight of fish caught from all trips,
W_i = weight of fish caught on trip i,
W_{ij} = weight of fish for sort j caught in trip i,
m_{ij} = number of clusters sampled from sort j on trip i,
m_i = number of clusters sampled on trip i,
m = number of clusters sampled over n trips,
$W_i = \sum_{j}^{L_i} W_{ij}$ where L_i is the number of sorts in trip i,
y_{ijk} = number of fish of the species in cluster k from sort j of trip i,
Y_{ij} = total number of the species caught from sort j of trip i,
Y = total number of species caught from all trips,
$\bar{\bar{Y}}$ = mean catch per cluster for the species,
$\bar{y}_{ij} = \sum_{k} y_{ijk}/m_{ij}$ = unbiased estimate of $\bar{Y}_{ij}$,
w_{ijk} = weight of the kth cluster from the jth sort of the ith trip,
$\hat{M}_i = \frac{W_i}{\bar{w}_i}$ where $\bar{w}_i = \sum_{j}\sum_{k} w_{ijk}/\sum_{j} m_{ij}$ =

average weight of sampled clusters in the ith trip.

If $\bar{W}_i$ is a constant, its estimate $\bar{w}$ will be given by $\bar{w} = \sum_i \sum_j \sum_k w_{ijk} / \sum_i \sum_j m_{ij}$. In practice, N and M_i will not be known and will be estimated by $\hat{N} = \frac{nW}{\sum_n W_i} = W/\hat{\bar{W}}$; $\hat{M}_i = \frac{W_i}{\bar{w}}$ respectively, if $\bar{W}_i$ is a constant $= \bar{w}$ (say).

Ratio Estimates of Mean and Total

The ratio estimate of mean catch ($\bar{\bar{Y}}$) per cluster is

$$\hat{\bar{\bar{Y}}}_R = \frac{\sum_i^n M_i \bar{y}_i}{\sum_i^n M_i} \doteq \frac{\sum_i^n W_i \bar{y}_i}{\sum_i^n W_i} \qquad (1)$$

where $\bar{y}_i = \sum_j M_{ij}\bar{y}_{ij} / \sum_j M_{ij} \cong \sum_j W_{ij}\bar{y}_{ij} / \sum_j W_{ij}$.

The ratio estimate of total catch Y is

$$\hat{Y}_R = \frac{W}{\bar{w}} \hat{\bar{\bar{Y}}}_R. \qquad (2)$$

The above estimators recommended for use are not workable in rockfish sampling because the sampler failed in almost all cases to subsample from more than one category in a sampled trip as would be seen from a sample of basic data for 1982 (Table 1) available for Eureka from the Department of California Fish and Game. The reasons for failure to collect the data are discussed in the section on Collection of Representative Data-Measurement Errors. The above estimators are, however, recommended for use in situations where the problem does not exist and, in particular, for single species where the categories are based on size. The estimates of error are given in Equations (4) and (5).

TABLE 1.—Distribution of landing weights (lb) from all categories and from the sampled category for Eureka for 1982.

Sample no. (boat trip)	Number of clusters sampled (m_i)	Market category sampled[1]	Weight of all fish (W_i) in a given trip	Weight of all fish for the category in a given trip
1528	1	269	26,550	24,176
1529	1	250	4,133	445
1530	2	269	59,218	58,239
1531	1	269	20,511	15,987
1533	1	269	35,022	14,661
1534	1	269	20,757	20,705
1535	1	269	15,812	8,436
1536	1	250	1,975	1,010
1537	1	250	16,055	1,075
1541	3	269	65,837	65,837

[1]Shows the code number of categories which are based on species, size, and quality.
Note: In all cases, only one of the categories could be sampled from a given trip. In boat 1541 there was only one category (269) of fish.

Estimation Ignoring Category Variation Within Sampled Trips

Assume that a cluster is selected at random from all possible clusters in a sampled trip. In other words, we ignore categories altogether both in sample selection as well as in estimation. Valid ratio estimates $\hat{\bar{\bar{Y}}}_{1R}$ of $\bar{\bar{Y}}$ and $\hat{Y}_{1R}$ of Y are respectively given by

$$\hat{\bar{\bar{Y}}}_{1R} = \frac{\sum_i^n W_i \bar{y}_i}{\sum_i^n W_i}; \quad \hat{Y}_{1R} = \frac{W}{\bar{w}} \hat{\bar{\bar{Y}}}_{1R}. \qquad (3)$$

Note these equations are essentially the same as Equations (1) and (2) except that we now assume that a cluster is randomly selected from all possible clusters in a sampled trip where W_i is the total landing weight from all categories for the ith boat trip in the sample ($W = \sum_i W_i$). In practice, the sampler would tend to subsample from a category which is accessible and is preponderant. This may lead to some bias in the estimate though its contribution to the total error will be negligible, since this would occur at the second stage of sampling.

The estimates of variance of estimated total and mean are approximately given by

$$v(\hat{Y}_{1R}) \doteq \left[\frac{1}{n}(1 - f_1)s_b^2 + \frac{f_1(1 - \bar{f}_2)s_w^2}{n\bar{m}}\right]\left(\frac{W}{\bar{w}}\right)^2 \qquad (4)$$

$$v(\hat{\bar{\bar{Y}}}_{1R}) \doteq \left(\frac{\bar{w}}{W}\right)^2 v(\hat{Y}_{1R}) \qquad (5)$$

where $s_b^2 = \sum_i^n \left(\frac{W_i}{\hat{\bar{W}}}\right)^2 \frac{(\bar{y}_i - \hat{\bar{\bar{Y}}}_{1R})^2}{n - 1}$;

$$s_w^2 = \sum_i^n \frac{\bar{m}}{n}\left(\frac{W_i}{\hat{\bar{W}}}\right)^2 \frac{s_{2i}^2}{m_i} \qquad (6)$$

and $s_{2i}^2 = \sum_k^{m_i} (y_{ik} - \bar{y}_i)^2/(m_i - 1)$; $\hat{\bar{W}} = \sum^n W_i/n$;

$$f_1 = \sum^n W_i/W; \bar{f}_2 = \frac{\bar{w} \sum_i^n \frac{m_i}{W_i}}{n}. \quad (7)$$

We will consider an operationally feasible plan in which sample trips at a port during a month are poststratified into categories and clusters are subsampled from each category; where one or more categories are missed due to inadequate field staff and/or management problems, clusters should be selected from other boat trips containing the missed categories.

Assuming that the cluster weight of the unequal cluster size varies over trips, i.e., $\bar{w}_i = \sum_j \sum_k w_{ijk}/\sum_j m_{ij}$ estimates of mean and total are

$$\hat{\bar{\bar{Y}}}_{2R} = \frac{\sum_i^n W_i \hat{R}_i}{\sum_i^n W_i/\bar{w}_i}; \hat{Y}_{2R} = W \frac{\sum_i^n W_i \hat{R}_i}{\sum_i^n W_i} \quad (8)$$

where $\hat{R}_i = \frac{\bar{y}_i}{\bar{w}_i}$; $v(\hat{Y}_{2R})$ and $v(\hat{\bar{\bar{Y}}}_{2R})$ can be obtained similar to Equations (4) and (5).

Estimation Based on Categories as Domains of Study

This method is almost as precise as proportional stratified sampling if within each port-month stratum (a) a minimum of four landings or boat trips ($n_j \geq 4$) is selected for each category and (b) the landing weights are available by categories after the season to serve as weights at the estimation stage. The minimum number in (a) is mainly based on limitations of field staff and budget restrictions. The ratio estimates of mean catch per cluster, total catch, and their errors, assuming clusters of equal size and using categories as domains of study are given by

$$\hat{\bar{\bar{Y}}}_{3R} \doteq \sum_j W_j \bar{\bar{y}}_j / \sum_j W_j; \hat{Y}_{3R} \doteq \sum_j \hat{Y}_j \quad (9)$$

where $\bar{\bar{y}}_j = \sum_i^{n_j} W_{ij} \bar{y}_{ij} / \sum_i^{n_j} W_{ij}$ (10)

$$\hat{Y}_j = \bar{\bar{y}}_j \frac{W_j}{\bar{w}} \quad (11)$$

$$v(\hat{\bar{\bar{Y}}}_{3R}) \doteq \sum_j \frac{W_j^2}{W^2} v(\bar{\bar{y}}_j) + 2 \sum_j \sum_{<k} \frac{W_j W_k}{W^2} \operatorname{cov}(\bar{\bar{y}}_j, \bar{\bar{y}}_k) \quad (12)$$

and

$$v(\hat{Y}_{3R}) \doteq v(\hat{Y}_j) + 2 \sum_j \sum_{<k} \operatorname{cov}(\hat{Y}_j, \hat{Y}_k). \quad (13)$$

Both $v(\bar{\bar{y}}_j)$ and $v(\hat{\bar{\bar{Y}}}_{3R})$ are of standard forms and can be obtained as in Equation (4). Similarly, $v(\hat{Y}_j)$ and $v(\hat{Y}_{3R})$ can be obtained. The covariance terms in Equations (12) and (13) are ignored when the subsamples from different categories are from different boat trips and are, therefore, independent. In rockfish sampling this was found true, because the sampler failed in almost all cases to subsample from more than one category. In general, for all fish where sampling from more than one category per boat trip is feasible, e.g., with few species-size-qualities, Equation (13) should be used.

Assume that the clusters vary in size over trips. For any sort (say j)

$$\hat{Y}_{j_1} = \left[\sum_i W_{ij} \hat{R}_{ij} / \sum_i W_{ij} \right] W_j = \hat{R}_j W_j \quad (14)$$

and

$$\hat{\bar{\bar{y}}}_{j_1} = \sum_i W_{ij} \hat{R}_{ij} / \sum_i W_{ij} / \bar{w}_{ij} \quad (15)$$

where $\hat{R}_{ij} = \frac{\bar{y}_{ij}}{\bar{w}_{ij}}$; $\hat{R}_j = \sum \hat{R}_{ij} W_{ij} / \sum_i W_{ij}$. (16)

If n_j is small compared to N_j and if the same subsampling strategy is applied to each of the sample landings, we have, ignoring contribution due to second-stage sampling units,

$$v_1(\hat{R}_j) = \frac{1}{n_j(n_j - 1)} \sum_i \left[\frac{W_{ij}}{\hat{\bar{W}}_{ij}} \right]^2 (\hat{R}_{ij} - \hat{R}_j)^2. \quad (17)$$

Another estimator $v_2(\hat{R}_j)$ is the jackknife

$$v_2(\hat{R}_j) \doteq \frac{(n_j - 1)}{n_j} \sum_i (\hat{R}'_{ij} - \hat{R}'_j)^2 \quad (18)$$

$$\text{where } \hat{R}'_{ij} = \frac{\hat{R}_{1j}W_{1j} + \ldots + \hat{R}_{(i-1)j}W_{(i-1)j} + \hat{R}_{(i+1)j}W_{(i+1)j} + \ldots + \hat{R}_{nj}W_{nj}}{W_{1j} + \ldots + W_{(i-1)n_j} + W_{(i+1)n_j} + \ldots + W_{n_j}} \qquad (19)$$

$$\text{and} \quad \hat{R}'_j = \frac{1}{n_j}\sum_i R'_{ij}.$$

Thus $\hat{R}'_{ij}$ is obtained by omitting trip i from the sample for sort j and calculating $\hat{R}_{ij}$ instead of $\hat{R}_{ij}$ as in Equation (16).

Hence, for category j of a species

$$v(\hat{Y}_{j_1}) = W_j^2 v_1(\hat{R}_j)$$

or

$$= W_j^2 v_2(\hat{R}_j) \qquad (20)$$

where $v_1(\hat{R}_j)$ and $v_2(\hat{R}_j)$ are given by Equations (17) and (18).

For estimate of total over all sort groups for a species

$$\hat{Y}_{4R} = \sum_j \hat{Y}_{j_1} \qquad (21)$$

$$v(\hat{Y}_{4R}) = \sum_j v(\hat{Y}_{j_1}) + 2\sum_j \sum_{<k} \text{cov}(\hat{Y}_{j_1}, \hat{Y}_{k_1}) \qquad (22)$$

A simpler formula $v(\hat{Y}_{4R}) \doteq \sum_j v(\hat{Y}_{j_1})$ can be used where subsamples from different categories are from different boat trips and are, therefore, independent.

It is, however, more reasonable to assume that the frequency distribution of fish caught is more uniform within a category so that cluster weight would be approximately a constant within a category. If so, the estimates of mean and total are given by

$$\hat{\bar{Y}}_{5R} = \sum_j W_j \bar{\bar{y}}_j / \sum_j W_j; \; \hat{Y}_{5R} = \sum_j \hat{Y}_j \qquad (23)$$

where $\bar{\bar{y}}_j = \sum_i W_{ij}\bar{y}_{ij} / \sum_i W_{ij}$;

$$\hat{Y}_j = \frac{\sum_i W_{ij}\bar{y}_{ij}}{\sum_i W_{ij}} \frac{W_j}{\bar{w}_j} \qquad (24)$$

and $\bar{w}_j$ is the simple mean weight of clusters in the jth group. Where the assumption of constant cluster weight within a category is not valid, the more general results given in Equations (14) and (15) should be used.

Comparison of Methods: Ignoring Category Variation Versus Poststratification by Categories

We will compare the efficiency of the estimators (3), ignoring variation due to categories, with the estimators (9), based on poststratification of landings by categories at a port during a month. The analyses were based on Eureka and Monterey data for 1982. The coefficients of variation (c.v.) of mean catch per cluster for a species based on categories as domains of study (method 2) were in almost all cases lower (Table 2) than ignoring category variation (method 1). Since method 1 results in underestimation of c.v.'s because sampling is actually based on a stratified random sample instead of a simple random sample, the increased precision of method 2 is all the more striking.

The c.v. of the estimated mean catch by sex-age groups for a species for which the number of sample landings were ≥10 (Table 3) were in all cases less for method 2 than for method 1. It may, however, be pointed out the c.v.'s are likely to be affected by factors such as growth, maximum age, and maximum size of fish. These have not been considered in this study. Thus, estimates based on categories as domains of study proved more efficient than ignoring categories altogether. Besides, method 2 has the added advantage of providing estimates by

TABLE 2.—Coefficient of variation (c.v., in percent) of mean catch by species at Eureka and Monterey based on the two methods during 1982.

Location and species	Sample size (number of boat trips sampled)	c.v. (%)	
		Method 1[1]	Method 2[2]
Eureka			
Widow rockfish	88	11.48	7.33
Chilipepper	88	30.83	32.12
Bocaccio	88	26.01	24.40
Monterey			
Widow rockfish	54	18.31	6.62
Chilipepper	54	15.68	13.92
Bocaccio	54	12.57	10.32

[1]Method 1, based on random categories (i.e., ignoring stratification by categories).
[2]Method 2, based on categories as domains of study.

TABLE 3.—Coefficient of variation (c.v., in percent) of mean catch by species-sex-age[1] group at Eureka and Monterey based on the two methods during 1982.

Eureka					Monterey				
Number of boat trips sampled	Sex	Age (yr)	c.v. (%) Method 1	c.v. (%) Method 2	Number of boat trips sampled	Sex	Age (yr)	c.v. (%) Method 1	c.v. (%) Method 2
				Widow rockfish					
17	M	7	19.71	18.83	10	F	13	39.98	24.29
18	F	7	13.50	10.94	10	F	12	35.16	20.49
				Chilipepper					
11	F	13	39.98	24.89	24	F	9	18.48	7.63
11	F	12	34.77	31.21	21	F	7	22.09	9.81
				Bocaccio					
15	M	6	30.10	19.82	14	M	7	27.46	12.45
19	F	6	35.87	32.45	20	F	7	24.34	10.06

[1]Age-sex groups for which primary sampling units (landings) are ≥10.

market categories which is of considerable economic importance.

COST FUNCTION

Consider the cost function

$$C = c_1 n + c_2 n \bar{m} \tag{25}$$

where c_1 is the average cost (in minutes) per boat trip due to transport, contact, and delay in making a contact, c_2 the average cost in data collection (identification of species, sex, length, otoliths, etc.) per cluster within clusters per boat trip and C is the total cost involved in visiting the primary sampling units (boat trips) and collecting data from the n boats with an average of $\bar{m}$ clusters per boat sampled. Data collected at Tiburon by the California Department of Fish and Game and the National Marine Fisheries Service show that c = 111.80 min, c_2 = 58.3 min so that $\frac{c_1}{c_2} = 2$ apply. However, from more recent studies conducted $\frac{c_1}{c_2} = 3$.

The components c_1 and c_2 were estimated at

Activity	*Percent*	*Mean (in minutes)*
Transport	50.0	81.7
Contact	5.0	8.7
Delay (off loading, etc.)	13.0	21.4
	68.0	111.8

Data collection	*Percent*	*Mean (in minutes)*
Species[1]	7.7	14.0
Sex, length	5.8	10.6
Otolith	10.8	19.7
Preparation time	7.7	14.0
	32.0	58.3

[1]Excluding samples dominated by single species.

Minimizing Equation (4) subject to Equation (25) for the optimum allocation we have

$$\bar{m}_{\text{opt}} = \frac{s_w}{\sqrt{s_b^2 - \frac{s_w^2}{\bar{m}}}} \sqrt{\frac{c_1}{c_2}}. \tag{26}$$

TABLE 4.—Optimum values of m for estimating species catch per cluster by categories for different variance and cost ratios, 1978.

Species	Category[1]	n	s_b^2	s_w^2	$\bar{m}$	$c_1/c_2 = \frac{m_{\text{opt}}}{2}$	$c_1/c_2 = 3$
Eureka							
Bocaccio	250	25	1.80	3.01	2.16	3.86	4.73
Chilipepper	250	13	24.45	3.13	1.92	0.52	0.64
Widow rockfish	250	11	59.49	8.71	2.46	0.56	0.68
Monterey							
Bocaccio	253	31	95.15	4.20	1.97	0.63	0.77
Chilipepper	253	33	43.71	4.16	1.94	0.45	0.55
Widow rockfish	253	12	22.38	4.66	2.00	0.68	0.84

[1]Code numbers of categories which are based on size, species and quality.

The variation among clusters (s_b^2) in different landings at Eureka and Monterey for 1978 was in almost all cases greater than between clusters within the same landings (Table 4); also the optimum number of clusters per boat for estimating species number was mostly unity. Data from other ports follow the same pattern. Since a minimum of two clusters is needed to provide an estimate of between cluster within trip variation, a subsample of two clusters per category per trip is recommended. In practice, it is preferable to select a systematic sample of clusters separated in time.

VARIANCE COMPONENTS: SPECIES-AGE AND LENGTH GROUPS

A two-level nested analysis of variance for length and age with unequal sample size for species based on sample landings at ports during 1979 (Table 5) shows that both the variation, because of length and age, was generally high among sample landings compared with clusters within landings. Also, variation between clusters was generally of the same order as within clusters, and the optimum number of clusters was $\leqslant 2$. Data for other ports and years (not shown in the table) mostly supported the findings.

On the whole, both the variation in species number (Table 4) as well as in length and age (Table 5) was consistently high among sample landings relative to between clusters within landings; also, variation among clusters was not significant compared with variation within clusters. Hence, for precise estimation of species number, length, and age composition for a category at a port during a season, data should be collected from a large number of landings and from few clusters (two) from a category within a sample landing.

RELATIVE EFFICIENCY OF ESTIMATORS USING POSTSTRATIFICATION

Consider the three estimators of total catch for a sort of a species at a port during a year. We will use the same selection procedure with poststratification by sorts but different estimation procedures.

$$\hat{Y}_j = \frac{N_j}{n_j} \sum_{i=1}^{n_j} \bar{y}_{ij} \tag{27}$$

$$\hat{Y}_j = \frac{\sum_{i}^{n_j} W_{ij}\bar{y}_{ij}}{\sum_{i}^{n_j} W_{ij}} \frac{W_j}{\bar{w}_j} \tag{28}$$

$$\hat{Y}_{j_1} = \hat{R}_j W_j \tag{29}$$

where $\hat{R}_j$ is given by Equation (16), $\bar{y}_{ij}$ is the simple mean of species number per cluster for sort j from the ith sample, $\hat{Y}_j$ is the same as Equation (24) with a constant cluster weight within a sort group, and $\hat{Y}_{j_1}$ is a more general estimator based on the assumption that cluster weight varies among trips. For $v(\hat{Y}_{j_1})$ use $W_j^2 v_2(\hat{R}_j)$ where $v_2(\hat{R}_j)$ is the jack-

TABLE 5.—Two-level nested ANOVA of length and age of species with unequal sample sizes by ports during 1979. MS = mean square; F = F-RATIO, Statistic; *P* = observed probablity level.

	Age				Length			
Source	df	MS	F	*P*	df	MS	F	*P*
Widow rockfish at Eureka								
Samples	15	34.45	4.75	<0.005		37.86	3.09	<0.025
Clusters (within samples)	13	7.25	1.19	0.35		12.27	1.43	~0.18
Within clusters	320	6.09				8.58		
Chilipepper at Monterey								
Samples	43	31.74	4.05	<0.001	48	145.20	4.02	<0.001
Clusters	39	7.84	1.80	~0.001	44	36.10	1.43	~0.035
Within clusters	320	4.35			971	25.25		
Bocaccio at San Francisco								
Samples	10	84.97	6.95	<0.001	10	317.88	6.98	<0.001
Clusters	15	12.23	1.20	~0.30	16	45.55	0.80	~0.75
Within clusters	225	10.20			227	57.11		

knife estimator of Equation (18) and for $v(\hat{Y}_j')$ see Sukhatme (1954). $\hat{Y}_j'$ is generally subject to considerable bias.

The c.v. of total catch of bocaccio, chilipepper, and widow rockfish for different categories by port-year groups (Table 6) show that the estimators $\hat{Y}_j$ and $\hat{Y}_{j_1}$ are highly efficient compared with $\hat{Y}_j'$; also, $\hat{Y}_j$ turns out to be slightly superior to $\hat{Y}_{j_1}$ since the jackknife estimator $v_2(\hat{Y}_{j_1})$ is an underestimate and does not take into account the contribution of the within component of variance. Thus, the empirical evidence supports strongly the use of the estimator $\hat{Y}_j$.

TABLE 6.—Coefficient of variation (in percent) of estimates of total catch of bocaccio, chilipepper, and widow rockfish per cluster by ports during 1978 and for different categories for the three estimators $\hat{Y}_j'$, $\hat{Y}_j$, and $\hat{Y}_{j_1}$.

Port	Category	Number of boat trips sampled	$\hat{Y}_j'$	$\hat{Y}_j$	$\hat{Y}_{j_1}$
		Bocaccio			
San Francisco	253	20	13.51	10.24	11.64
Fort Bragg	250	86	16.21	7.36	8.14
Monterey	253	31	12.07	17.93	19.51
Eureka	250	25	40.11	26.00	29.84
		Chilipepper			
Eureka	250	13	37.66	34.52	42.33
		Widow rockfish			
Monterey	250	12	111.20	43.47	68.29
Eureka	250	11	72.69	27.81	33.90

AGE-COMPOSITION: DOUBLE SAMPLING

Studies mentioned in the Introduction section have shown that since aging from otoliths of each individual fish in a sample is more expensive than an easily measured quantity such as length, it may pay 1) to choose a random subsample from the whole sample of length measurements for age determination or 2) stratify the sample according to length classes and choose a subsample from each class for age determination. The technique is profitable only if the correlation between length and age is fairly high.

It may be recalled that considerable bias is introduced by applying age-length keys developed during a year to subsequent years. Both Kimura (1977) and Westrheim and Ricker (1978) showed that age-length keys can yield most inefficient estimates of numbers-at-age with substantial overlap of lengths between ages. In the latter case the correlation between length and age will be low for the larger and the very small sizes. Consequently, we will need a higher sampling intensity at the tails to provide reliable estimates of age for such sizes.

In the construction of length strata for selection of the subsample, additional questions arise on 1) number of strata to choose, 2) strata boundaries to decide, and 3) the number of sampling units to be allocated to each stratum for deriving maximum gain from double sampling. These are discussed as follows.

Number of Strata

The values of $V(\bar{y}_{st})/V(\bar{y})$ (Cochran 1977) are given below as a function of L, the number of strata using the linear model

$$y = \alpha + \beta x + \varepsilon \tag{30}$$

where y is the length, x the age of female widow rockfish and

$$\frac{V(\bar{y}_{st})}{V(\bar{y})} = \frac{\rho^2}{L^2} + (1 - \rho^2) \tag{31}$$

where ρ is the correlation between length and age in the unstratified sample and L the number of strata. It can be shown for this model that when $L \geq 6$ and $\rho > 0.95$, there is hardly any gain due to stratification (Table 7). The improvement in stratification is highest for data set 1 for which $\rho^2 = 0.7004$ and lowest for set 3 for which $\rho^2 = 0.5278$. The results for the regression model indicate that unless ρ exceedes 0.95, little reduction in variance is to be expected beyond $L = 6$. Data sets 1, 2, and 3 support this conclusion. In fact, there does not seem to be any profit resulting from increase in strata beyond $L = 5$.

Strata Boundaries

For the length-age strata on 239 females (widow rockfish) landed during 1982 at San Francisco and the rule based on the cumulative of $\sqrt{f(y)}$ (Cochran 1977) where y denotes the length in centimeters, the nearest available points for the two strata are

	Stratum 1	2
Boundaries	36-47 cm	48-55 cm
Intervals on cum $\sqrt{f}$	18.70	23.72

TABLE 7.—$V(\bar{y}_{st})/V(\bar{y})$ as a function of L for the linear regression and for some actual data.

	Linear regression model ρ =				Data set		
L	0.99	0.95	0.90	0.85	1	2	3
2	0.265	0.323	0.392	0.458	0.4747	0.5114	0.6041
3	0.129	0.198	0.280	0.358	0.3774	0.4209	0.5308
4	0.081	0.154	0.241	0.323	0.3434	0.3892	0.5052
5	0.059	0.134	0.222	0.306	0.3276	0.3746	0.4933
6	0.047	0.123	0.212	0.298	0.3154	0.3740	0.4890
∞	0.020	0.098	0.190	0.277			

		Type of data		
Set	Data	x Age (yr)	y Length (cm)	Source
1	Female widow rockfish (532) Monterey, San Francisco and Bodega Bay	1982 (Jan.-Mar.)	1982 (Jan.-Mar.)	Department of California Fish and Game and Tiburon Laboratory
2	Female widow rockfish (444) Eureka	1981 (Jan.-Sept.)	1981 (Jan.-Sept.)	
3	Female widow rockfish (328) Eureka	1980 (Apr.-Dec.)	1980 (Apr.-Dec.)	

It turns out that the division point is approximately the same for young as well as old widow rockfish.

For length-age data (1981) based on 444 females (widow rockfish) landed at Eureka, the boundaries using 2 and 3 strata are

	Stratum	
	1	2
Boundaries	31.5-47 cm	46.5-55 cm
Intervals on cum $\sqrt{f}$	17.70	29.01

	Stratum		
	1	2	3
Boundaries	31.5-46 cm	46.5-49 cm	49.5-55 cm
Intervals on cum $\sqrt{f}$	17.70	13.12	15.89

Optimum Allocation Plan

Double sampling with regression is more efficient than single sampling (when the first sample is measured for age alone) for the same cost if

$$\rho^2 > \frac{4\frac{c}{c'}}{\left[1 + \frac{c}{c'}\right]^2} \qquad (32)$$

where ρ is the correlation between length and age of fish, c and c' are respectively the costs of aging and measuring a fish. Assuming that the average cost of aging a rockfish (including small and large fish) is 6 min and of measuring it is 1.2 min (estimates based on measurements by W. Lenarz of Tiburon Laboratory), we have from Equation (32)

$$\rho^2 > 0.5555$$

or

$$\rho > 0.7453.$$

For the three data sets (Table 7) the values of ρ^2 are respectively 0.7004, 0.6515, and 0.5278 so that Equation (32) is approximately satisfied. However, neither ρ nor $\frac{c}{c'}$ are large enough to suggest that double sampling will be much more efficient than single sampling.

We will illustrate the use of double sampling for stratification by analyzing 1981 length-age data at Eureka to estimate the proportion of female in age group 11, based on a sample of 444 fish. For the three length strata, $h = 1, 2, 3$ with stratum boundaries based quadratic fit of length on age are 31.5-43, 43.5-49, 49.5-55. (Note this is different than boundaries based on length only.) Also

c_0 = 1.2 min, c_1 = 3.8 min, c_2 = 3.8 min, and c_3 = 8 min
w_1 = 0.0653, w_2 = 0.5451, and w_3 = 0.3896
s_1 = 0.1825, s_2 = 0.4966, s_3 = 0.1503,
and s = 0.4343

where w_1, w_2, and w_3 are the proportions of fish in the sample, c_0 is the cost of measuring a fish and c_1, c_2, c_3 are respectively the costs of aging them in the three length groups. From Cochran (1977, p. 331) we have

$$v_{\min}(p_{st}) = \frac{1}{C^*}\left[\sum w_h s_h \sqrt{c_h} + (S^2 - \sum w_h s_h^2)^{1/2}\sqrt{c'}\right]^2 \qquad (33)$$

$$= 0.8915/C^*$$

where p_{st} is the estimated proportion and $C^* = E(c) = E(c_0\, n + \sum_n c_h n_h)$ with $n_1 = 14$, $n_2 = 120$, $n_3 = 48$ and $n' = 444$. The efficiency of double sampling with respect to single sampling is given by

$$v_{srs}(p)/v_{\min}(p_{st}) = 1.27$$

where $v_{srs}(p) = 0.1885/\frac{C^*}{6}$, i.e., double sampling is 27% more efficient than single sampling. However, as noted by Ricker (1975) the increase in accuracy achieved by combining a length sample with a smaller age sample may not be great unless fish used for age determination is taken from the same stock, during the same season and using gear having the same selective properties as the length-frequency samples. This point will generally be met if fish are subsampled systematically for age from fish arranged in increasing (or decreasing) order of length from a port-month stratum. Our studies have shown that the best length-age fit does not change significantly if age determination is made on every other fish arranged in ascending order of length.

It is difficult to obtain reliable estimates of the numbers at age for the extremely small or larger sizes because lengths cannot be used for estimating age. There is need for search for other auxiliary variables (other than length) associated with age and for increase in sampling rate at the tails. In double sampling where lengths are obtained in the first phase, a number of small clusters may be used separated in space and time to provide a large number of fish at the tails for estimating numbers at age. The extent of bias in estimation of numbers at age through length-age key approach may be tested by Monte Carlo simulation.

COLLECTION OF REPRESENTATIVE DATA-MEASUREMENT ERRORS

Owing to uncertainty of arrival times and varying unloading procedures, no objective method is available to ensure random sampling of the trips. When the vessels return to port, they are usually available for sampling except when they are transhipped immediately due to inclement weather, lack of processing facilities, uncooperative buyers, or unscheduled deliveries at short notice. It is, however, not unreasonable to regard a set of sample landings during a week at a port as random and representative of the totality of all landings at the port for the month.

Although rockfish are landed by categories, which are mostly determined by market agreement based on size, composition, and condition of the catch, the number of categories per delivery cannot be predetermined. This number would vary from delivery to delivery and from dealer to dealer. Also, there are no guarantees that a complete boat sample, covering clusters from each category, can be taken on any sampling day and some of the categories are actually missed in sampling. Some of the possible reasons for missing the categories are 1) when landing weight would not occur during regular hours, one of the sorts may have already been shipped before the sample could arrive at the spot; 2) often one of the sorts may be quite small and there may be a buyer at the dock waiting for the fish to be taken away; 3) while the sampler is working on a sort, the other sort(s) will have either been processed or shipped away; and 4) the sampler may

be prevented from taking a sample from another sort by the skipper who may not like some of his fish being cut and otoliths removed for biological studies. This may happen at ports where either processing facilities are inadequate or fish are bought by local merchants immediately after landing. The question arises if failure to sample from all categories of a sample landing as originally planned would cause appreciable bias and loss in efficiency in the estimates of species catch and its distribution and whether a more efficient method could be developed that is operationally feasible. This point has been examined in the present paper.

The present technique of selecting a cluster (box) of fish as second stage sampling unit is preferred to random selection of a specified number of individual fish because in practice the potential of personal bias of the sampler could be considerable. Often fish chosen by the latter technique are ones closest to the sampler or those that fell in a certain position. Tomlinson (1971) felt that in this approach the sampler may tend to choose a fish with certain qualities and thus may introduce procedural bias.

The selection of a representative cluster would depend whether samples after sorting on the vessel come from bins, strap boxes, or off conveyor belts. Buyers from small markets occasionally select fish from the top of bins. Hence, to avoid this bias, it is preferable to select the cluster from the conveyor belt which exposes unsorted fish from the lower portion of the bin. However, where small market buyers do not buy fish, a cluster may be selected from a bin. Where many bins are present a systematic sample of two clusters, preferably from the beginning and end of the trip may be selected. Where fish are graded on a conveyor belt before they enter the plant (e.g., Fieldslanding at Eureka) the sampler should try to intercept the landings prior to secondary sorting or obtain separate weights for each subsort category. In general, selection of a cluster for a market category should be done before any presorting is done at the port.

It has been pointed out earlier that bias may result from personal selection of fish within a cluster. If the sampler were to select a number of clusters with few fish per cluster, a cluster will on the average contain more big fish. This would lead to high nonsampling bias. Sometimes, the top few fish in a bin are selected and put there to impress small buyers. The resulting bias in selection can be avoided by taking all the fish in a cluster (e.g., 50 lb) from one side of the box.

For obtaining reliable and comprehensive information on population characteristics, it is essential for the sampler to maintain good relationships with both the skipper and the buyer; this will depend to a large extent on the expertise of the sampler gained in the course of the field work.

SUMMARY

1. The sampling scheme at a port during a month with poststratification of sampled trips into categories and subsampling of clusters from each category (see sections on Estimation with poststratification and Estimation ignoring category variation) is not workable for estimating rockfish catch since some of the categories may be missed in sampling due to inadequate field staff and/or management problems.
2. For other commercial fish where the above problem does not exist and landing weights by categories are not available at the end of the season, the methods (see sections on Estimation with poststratification and Estimation ignoring category variation) are recommended, e.g., for single species where the categories are based on size.
3. For estimating the catch of rockfish, a two-stage sampling plan is recommended with boat trips as first stage units poststratified into categories and clusters subsampled from a category; estimates are based on categories as domains of study with landing weights available for each category. A minimum of four landings or boat trips should be used for each category, to provide efficient estimates. With few categories, this number is likely to be large.

   Where only one category is subsampled for each boat in the sample, $v(\hat{Y}_{3R}) = \sum_j v(\hat{Y}_j)$. In all other cases Equation (13) should be used.
4. The design described in the above paragraph is recommended for use in other fisheries where landing weights are available for each category. Equations (9) and (21) are recommended for the estimation of catch according as the clusters are of equal or unequal size. Equations have been provided for the more practical case when cluster weight can be treated as constant within a category but different among categories.
5. Estimates of species catch by sex and age based on method 1 are less efficient than those based on method 2 which is based on categories as domains of study (Tables 2, 3).
6. Method 2 is preferred to method 1 when there

is variation among categories. This is true for all fish.

7. With few categories (species-size-qualities) the chance of missing a category is reduced. Equations (9) and (13) should be used for clusters of equal size and Equations (21) and (22) for unequal size clusters. This result is, of course, applicable to all commercial fish.
8. As far as practicable, selection of a cluster for a market category should be done before any presorting is done at the port either from bins, strap boxes, or off conveyor belts.
9. Variation (within categories) in length and age for a species was considerably higher among boat trips than among clusters within boat trips. Also, variation among clusters was not significant, compared with variation within clusters (Table 5). Hence, for precise estimation of species number, length, and age composition for a category at a port during a season data should be collected from a large number of landings and from few clusters from a category within a sample landing. This result should hold for all commercial fish.
10. For the cost function $C = c_1 n + c_2 n\bar{m}$ where c_1 is the average cost (in minutes) per boat trip due to transport, contact, and delay in making a contact, c_2 the average cost of data collection (identification of species, sex, length, otoliths, etc.) per cluster per boat trip and C is the total cost involved in visiting the primary sampling units (boat trips) and collecting data, the optimum number of clusters per sampled trip for a fixed cost for a category is two (Table 4). This should provide valid estimates of error as required in Equations (13) and (22).
11. The principal contribution of the paper is that a minimum of four sample landings be subsampled for each category from a port-month stratum, i.e., about 1 per week and two clusters of 50 lb (25 lb for small fish) each should be sampled to provide port-year estimates with a reasonable degree of accuracy.

    If a category is infrequently landed, sampling should be directed towards the infrequent category, as long as the number of landings for the category is less than four per month.
12. The efficiency of the ratio estimator (Equation (28)) based on poststratification by categories at port-year level and using constant cluster weight within a category was compared with two other estimators, including the ratio estimator based on jackknife. Empirical evidence indicated that the ratio estimator using constant cluster weight within a category proved most efficient for estimation of species catch.
13. Age-length keys can yield most inefficient estimates of the numbers at age for extremely small and large fish. It is suggested that cluster sampling for length be based on a number of clusters separated in space and time; also, sampling for age should be intensified for small and large fish. This approach is applicable to all fish.
14. Double-sampling was adopted for estimating proportion of widow rockfish in 11-yr age group. A sample of fish was divided into 3 strata and optimum allocation for age was adopted within strata. The estimated proportion was 27% more efficient than if single sampling were adopted.

The best length-age did not change significantly if age determination is made on every other fish selected in ascending order of length.

The method is general and is applicable to all fish.

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A VARIABLE CATCHABILITY VERSION OF THE LESLIE MODEL WITH APPLICATION TO AN INTENSIVE FISHING EXPERIMENT ON A MULTISPECIES STOCK

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ABSTRACT

A variable catchability version of the Leslie model is developed which permits the catchability of one species to vary inversely with the abundance of competing species. This model is used to fit data from an intensive fishing experiment conducted on a multispecies bottom fish stock in the Marianas where catchability of a subordinate species is inversely related to the abundance of a more dominant species. Analysis of this multispecies intensive fishing experiment produced estimates of exploitable bottom fish density in the 150-275 m depth range of 10,156 fish per nmi^2 or 1,354 fish per nmi of 183 m (100-fathom) contour.

Intensive fishing of a closed population can produce data to estimate the initial population size and the catchability coefficient of fish stocks. Two frequently used models applied to intensive fishing data are the Leslie model and the Delury model (Ricker 1975). The Leslie model expresses catch per unit effort (CPUE) at any point during the period of intensive fishing as a linear function of the cumulative catch to that point, whereas the Delury model expresses the logarithm of CPUE at any point during the intensive fishing experiment as a linear function of the cumulative effort. From a statistical viewpoint the Leslie model is often preferable to the Delury model, since a predictive linear regression is used to estimate the parameters of both models and since typically catch is measured more accurately than effort.

Both the Leslie and Delury models assume that catchability is constant during the period of intensive fishing. However, experience indicates that this assumption may not always be satisfied (Pope and Garrod 1975; Schaaf 1975; MacCall 1976; Ulltang 1976; Garrod 1977; Peterman and Steer 1981; Fox[2]). Several authors have found that competition for baits between fish of different size or species can alter catchability (Allen 1963; Rothschild 1967). In this paper a variable catchability Leslie model will be developed for multispecies application where, due to species interactions, the catchability of one species is altered by the presence of other species. This variable catchability Leslie model will be applied to multispecies intensive fishing data from snapper (family Lutjanidae) populations where the application of the constant catchability Leslie model leads to biologically untenable results.

VARIABLE CATCHABILITY LESLIE MODEL

The CPUE during a time interval t (CPUE(t)) is defined as the product of catchability (q) and the mean population size (number of individuals) present during the period t ($N(t)$), thus

$$\text{CPUE}(t) = qN(t). \quad (1)$$

Suppose that up to the beginning of period t, $K(t)$ fish have been caught and removed. If the period t is relatively short, the population of fish closed or isolated, and the fishing pressure heavy enough so that it can be assumed that mortality from other factors is negligible, then $N(t)$ can be expressed as

$$N(t) = N(0) - K(t),$$

where $N(0)$ is the initial population size at the beginning of the experiment ($t = 0$). Inserting this expression for $N(t)$ in Equation (1) produces the Leslie model:

$$\text{CPUE}(t) = q(N(0) - K(t)). \quad (2)$$

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[2]Fox, W. W. 1974. An overview of production modelling. U.S. National Marine Fisheries Service, Southwest Fisheries Center, Administrative Report LJ-74-10, La Jolla, CA.

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Henceforth, this model will be referred to as the constant catchability Leslie model.

In a multispecies situation, competition between species for baited hooks may produce a dominance hierarchy where some species are more aggressive feeders than others and effectively out compete the less aggressive feeders for baited hooks. The catchability of the species at the top of the dominance hierarchy, is independent of the presence of more subordinate species, while the catchability of those species not at the very top of the hierarchy will vary inversely with the abundance of the more dominant species. A simple model which describes the catchability of a subordinate species ($q(s,t)$) as a function of the cumulative catch and initial population size of the more dominant species, $K(d,t)$ and $N(d,0)$ respectively is

$$q(s,t) = q(s)(K(d,t)/N(d,0)) \quad (3)$$

where $q(s)$ is the catchability of the subordinate species in the absence of the dominant species. Combining Equations (2) and (3) produces

$$\text{CPUE}(s,t) = q(s)(K(d,t)/N(d,0)) \times (N(s,0) - K(s,t)) \quad (4)$$

and by defining $K(ds,t) = K(d,t)K(s,t)$, $B1 = q(s)(N(s,0)/N(d,0))$, and $B2 = q(s)/N(d,0)$ Equation (3) becomes

$$\text{CPUE}(s,t) = B1K(d,t) - B2K(ds,t).$$

Estimates of $B1$ and $B2$ are obtained from multiple linear regression and the estimates of $N(s,0)$ and $q(s)$ are computed as

$$\hat{N}(s,0) = \hat{B}1/\hat{B}2, \text{ and } \hat{q}(s) = \hat{N}(d,0)\hat{B}2.$$

The estimate of $N(d,0)$ is determined from the constant catchability model. As is evident from Equation (4), the estimate of $N(s,0)$ is independent of the estimate of $N(d,0)$. Estimates of the variance of the estimate of $N(s,0)$ are obtained from estimates of the means and variances of the estimates of $B1$, and $B2$ and an exact expression for the variance of a ratio (Frishman 1975). Thus,

$$V(\hat{N}(s,0)) = V(\hat{B}1/\hat{B}2) = \frac{V(\hat{B}1)[E(\hat{B}2)]^2 - V(\hat{B}2)[E(\hat{B}1)]^2}{(E(\hat{B}2))^2\,[V(\hat{B}2) + [E(\hat{B}2)]^2]} \quad (5)$$

where $V(\ )$ and $E(\ )$ represent the variances and means, respectively.

APPLICATION OF MULTISPECIES LESLIE MODEL TO SNAPPER INTENSIVE FISHING

A 13-d intensive fishing experiment covering the period 10-19 April and 5-7 May 1984 was conducted at Pathfinder Reef (lat. 16°30′N, long. 143°05′E) in the Mariana Archipelago. Pathfinder Reef is a circular pinnacle rising steeply from a depth of about 1,600 to 16 m beneath the surface. At the 200 m contour, the diameter is about 0.8 nmi (Fig. 1). The snapper population at Pathfinder Reef is a closed population for purposes of the intensive fishing since the closest bank is a small pinnacle 40 nmi to the north.

Intensive fishing was conducted from the NOAA ship *Townsend Cromwell* using four bottom handlines on hydraulic gurdies targeting species in the 150-275 m depth range. Each day during the 13-d experiment, fishing was conducted around the entire perimeter of the bank. During the experiment 1,467 bottom fish were caught. Three lutjanids, *Pristipomoides zonatus*, *P. auricilla*, and *Etelis carbunculus*, accounted for 1,317 fish or about 90% of the catch (Table 1). Fishing effort was measured in

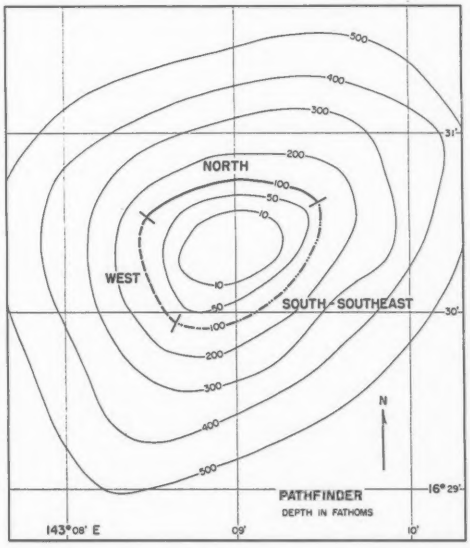

FIGURE 1.—Bathymetric chart of Pathfinder Reef showing the segments of the 100-fathom (183 m) contour used to partition daily fishing effort.

TABLE 1.—Species composition of bottom fish catch at Pathfinder Reef.

Species	Number caught	Percent of catch
Lutjanidae		
Aphareus rutilans	4	0.27
Aprion virescens	1	0.07
Etelis carbunculus	314	21.40
Pristipomoides auricilla	262	17.86
P. filamentosus	16	1.09
P. flavipinnis	7	0.48
P. zonatus	741	50.51
Carangidae		
Caranx lugubris	83	5.66
Seriola sp.	32	2.18
Serranidae		
Cephalopholis igarasiensis	2	0.14
Epinephelus cometae	2	0.14
Saloptia powelli	3	0.20
Total	1,467	100.00

line-hours. As is indicated in Figure 1, the circumference of the reef can be divided into three segments—north, west, and south-southeast, each having similar species composition (Table 2). Further, an attempt was made daily to allocate a consistent proportion of the day's fishing effort to each segment. The proportion allocated to each segment was influenced by the length of each segment and wind and current conditions. On the average, the proportion of the total daily effort allocated to each segment was 0.45 on the south-southeast, 0.21 on the north, and 0.34 on the west. A chi-squared test applied to the daily allocation of fishing effort indicates that there was no significant departure ($P = 0.89$) from this allocation during the course of the fishing experiment. Since the effort was reasonably constant over the duration of the experiment and the entire reef was fished each day, catch, effort, and CPUE computed on a daily basis were used in the analysis. An adjustment to cumulative catch suggested by Chapman (1961) was subsequently shown to improve the model fit in the Delury model (Braaten 1969). This adjustment computes cumulative catch for interval i as the cumulative catch to interval i plus one half the catch during interval i. This adjustment compensates for the decline in CPUE within each time interval. The adjusted cumulative catch is used as the independent variable in all subsequent analyses (Table 3).

TABLE 2.—Species composition for the three segments of the circumference of Pathfinder Reef (see Figure 1).

	South-Southeast		North		West	
Species	No.	%	No.	%	No.	%
Pristipomoides zonatus	358	51	160	68	223	58
P. auricilla	170	24	37	16	55	14
Etelis carbunculus	171	25	39	17	104	27

Plots of CPUE against adjusted cumulative catch for each of the three species of snappers show a decline in CPUE for *P. zonatus*, a slight decline for *E. carbunculus*, and an increase for *P. auricilla* (Fig. 2). A regression line fitted to these data results in negative slopes for *P. zonatus* ($P = 0.0007$) and *E. carbunculus* ($P = 0.05$) and a positive slope for *P. auricilla* ($P = 0.008$). The constant catchability Leslie model fitted the *P. zonatus* data well and resulted in an R^2 of 0.71 and a pattern of residuals which supports the linear model. The estimates of $N(0)$ and q for *P. zonatus* from this fit are 1,066 fish and 0.0038 per line-hour. Due to the selectivity of the fishing gear, $N(0)$ estimated from this intensive fishing data does not represent total population size

TABLE 3.—Daily catch, effort, catch per unit of effort (CPUE), and adjusted cumulative catch for *Pristipomoides zonatus*, *P. auricilla*, and *Etelis carbunculus*

		Total			*Pristipomoides zonatus*			*P. auricilla*			*Etelis carbunculus*		
Date 1984	Effort (line-hours)	Catch (no.)	CPUE	Adjusted cumulative catch	Catch (no.)	CPUE	Adjusted cumulative catch	Catch (no.)	CPUE	Adjusted cumulative catch	Catch (no.)	CPUE	Adjusted cumulative catch
Apr. 10	27.5	152	5.53	76	98	3.56	49	12	0.44	6	42	1.53	21
Apr. 11	23.7	150	6.33	227	111	4.68	153.5	17	0.72	20.5	22	0.93	53
Apr. 12	21.3	100	4.67	352	47	2.21	232.5	12	0.56	35	41	1.93	84.5
Apr. 13	29.7	139	4.68	471.5	91	3.06	301.5	29	0.98	55.5	19	0.64	114.5
Apr. 14	29.3	112	3.82	597.0	66	2.25	380	17	0.58	78.5	29	0.99	138.5
Apr. 15	17.5	84	4.80	695.0	50	2.86	438	13	0.74	93.5	21	1.20	163.5
Apr. 16	30.7	129	4.20	801.5	67	2.18	496.5	26	0.85	113	36	1.17	192.0
Apr. 17	21.4	65	3.04	897.5	38	1.78	548	12	0.56	132	15	0.70	217.5
Apr. 18	22.4	81	3.62	970.5	41	1.83	587.5	15	0.67	145.5	25	1.12	237.5
Apr. 19	21.6	60	2.78	1,041	28	1.30	622.0	17	0.78	161.5	15	0.69	257.5
May 5	20.3	82	4.04	1,112.5	40	1.97	656	29	1.43	184.5	13	0.64	271.5
May 6	22.8	91	3.99	1,199.0	35	1.54	693.5	35	1.54	216.5	21	0.92	288.5
May 7	24.1	72	2.99	1,281	30	1.25	726.0	27	1.12	248.5	15	0.62	306.5

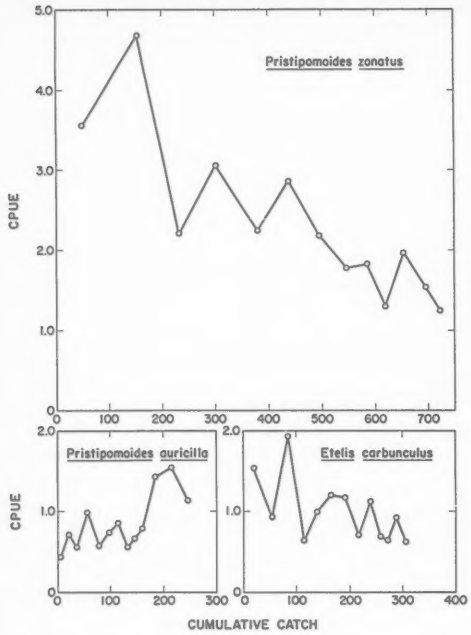

FIGURE 2.—Daily catch per unit effort (CPUE) and adjusted cumulative catch for *Pristipomoides zonatus*, *P. auricilla*, and *Etelis carbunculus*.

but rather the population size of those fish that can be caught by the fishing gear which will be termed the exploitable population. Although the constant catchability Leslie model does not explain as much of the variation for *E. carbunculus* (R^2 = 0.35) as it does for *P. zonatus*, the regression is significant and the pattern of residuals supports the linear fit. The estimates for catchability and initial exploitable population size for *E. carbunculus* from the fit of this model are 0.0025 per line-hour and 583 fish. The positive slope for the regression of CPUE on cumulative catch for *P. auricilla* does not make sense biologically under the constant catchability Leslie model.

The depth of capture data show that *P. zonatus* and *P. auricilla* were caught in the same depth range, whereas *E. carbunculus* was typically caught at somewhat greater depths (Table 4). Thus, species interactions would most likely occur between *P. zonatus* and *P. auricilla*. If *P. zonatus* is more aggressive than *P. auricilla* in pursuing fishing baits or in some other way affects the behavior of the latter, then the initial catchability for *P. auricilla* will

TABLE 4.—Percent of catch by depth (in fathoms, 1 fathom = 1.83 m).

Species	Depth		
	<100	100-120	>120
Pristipomoides zonatus	15.1	71.7	13.2
P. auricilla	12.6	79.0	8.4
Etelis carbunculus	1.9	46.5	51.6

be low but will rise as the population of *P. zonatus* is reduced. Applying the variable catchability Leslie model to the *P. auricilla* data, with the assumption that *P. zonatus* is the dominant species and that *P. auricilla* is the subordinate species so that the catchability of *P. auricilla* depends on the population size of *P. zonatus*, results in the following relationship:

$$\mathrm{CPUE}(a,t) = q(a)(K(z,t)/N(z,0)) \times (N(a,0) - K(a,t)), \quad (6)$$

where $q(a)$ is the catchability of *P. auricilla* in the absence of *P. zonatus* and $N(z,0)$ and $N(a,0)$ are the initial exploitable population sizes of *P. zonatus* and *P. auricilla*, respectively, and $K(z,t)$ and $K(a,t)$ are the cumulative catch of *P. zonatus* and *P. auricilla* to time t, respectively.

Using the estimate of $N(z,0)$, 1,066 fish, from the fit of the constant catchability model to *P. zonatus* data, Equation (6) has two unknowns to be estimated—$q(a)$ and $N(a,0)$. A multiple linear regression model estimates the initial exploitable population size of *P. auricilla*, $N(a,0)$, at 2,007 fish and $q(a)$ at 0.00087. The variable catchability Leslie model fits the *P. auricilla* CPUE data well and produces an R^2 of 0.89 (Fig. 3). The estimates of initial population sizes for the three species are summarized in Table 5 together with their 95% confidence intervals. For the constant catchability model, the population size confidence interval is computed from a relationship derived by Delury (1958), whereas the confidence interval for the variable catchability model is computed from the variance expression given in Equation (5).

DISCUSSION

The constant catchability Leslie model fit the *P. zonatus* and *E. carbunculus* data well but was not appropriate for the *P. auricilla* data. The variable catchability Leslie model fit the *P. auricilla* data well and provided a plausible explanation for the observed increase in CPUE. Given that there was a time delay between the first 10 d of the intensive

fishing (10-19 April) and the last 3 d (5-7 May), and that the greatest increase in the catchability of *P. auricilla* occurred after the time delay, it is possible that the increase in catchability might have a time lag component associated with it. However, given the short time series of data, it would be difficult to test the appropriateness of a more complicated time lag model.

Based on the fit of these two models the initial exploitable population of the three species in the 150-275 m depth range at Pathfinder Reef is estimated at 3,656 fish (Table 5). If we assume, based on the species composition data (Table 1), that these three species represent 90% of the exploitable population then the total exploitable population at the beginning of the intensive fishing is 4,062 fish.

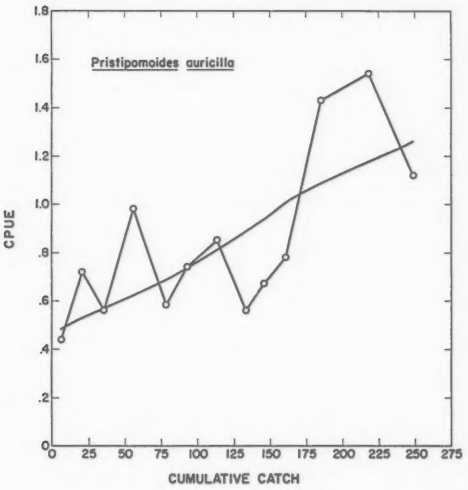

FIGURE 3.—Daily catch per unit effort (CPUE) and predicted CPUE based on the variable Leslie model as a function of adjusted cumulative catch for *Pristipomoides auricilla*.

From Figure 1 the length of the 183 m (100-fathom) contour is estimated at 3.0 nmi, and the area in the 180-300 m depth range is estimated to be 0.4 nmi^2. With these area measures, density estimates of 1,354 fish per nmi of (183 m) 100-fathom contour and 10,156 fish/nmi^2, are obtained for Pathfinder Reef.

Estimates of bottom fish densities based on visual observation from a submersible at Johnston Atoll were 57,281 fish/nmi^2 for the 92-183 m (50-100 fathom) depth range and 66,199 fish/nmi^2 for the 1983-274 m (100-150 fathom) depth range (Ralston et al. 1986). These figures are considerably larger than both the point and interval estimates presented here. Significantly, the study of Ralston et al. (1986) also employed the *Townsend Cromwell*, and the catch rates were comparable at Pathfinder and Johnston (e.g., 3.18 bottom fish/line-hour for the latter). Thus the difference between estimates of standing stock is likely not due to differences in absolute abundance but rather to differences between exploitable population size and total population size. For example, at Johnston Atoll at least 69 species of fish were observed from the submersible, whereas only 10 species were taken by fishing gear in the same depth (Ralston et al. 1986).

If the constant catchability Leslie model is applied to the pooled data for the three species, an estimate of exploitable population size of 2,689 is obtained, about 71% of the estimate of the exploitable population size for the three species when they are estimated separately (Table 5).

Size-specific behavior has been raised as a factor which might affect catchability (Allen 1963). For all three species, there is no evidence of intraspecies size-specific behavior affecting catchability since for two of the species the constant catchability model fits well and for the third species, catchability depends only on the population size of an interacting species. Further, under the hypothesis that within a stock catchability is size-specific across the

TABLE 5.—Estimates of population size and catchability for three species.

Species	Model	R^2	Catchability	SE	Initial population size	Confidence interval (95%)
Pristipomoides zonatus	Constant catchability	0.71	0.0038	0.0075	1,066	(803-1,691)
Etelis carbunculus	Constant catchability	0.35	0.0025	0.0010	583	(361-3,011)
P. auricilla	Variable catchability	0.89	0.00087	0.00031	2,007	(261-5,727)
Three species pooled	Constant catchability	0.66	0.0022	0.0047	2,689	(1,955-4,535)

range of exploitable size, intensive fishing would produce a substantial change in the population size structure. A plot of the mean fork length by day of fishing for the three species (Fig. 4) shows very little change in fork length even for *P. zonatus* where 68% of the exploitable stock is estimated to have been removed. Thus, the mean size of the fish in a catch may be a much less sensitive indicator of changes in the population size than catch rates, at least over the short term.

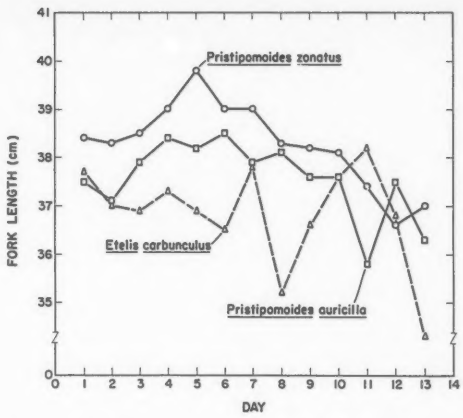

FIGURE 4.—Mean fork length for each day of fishing for *Pristipomoides zonatus*, *P. auricilla*, and *Etelis carbunculus*.

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EARLY DEVELOPMENT OF THE LOPHIID ANGLERFISH, *LOPHIUS GASTROPHYSUS*

YASUNOBU MATSUURA AND NELSON TAKUMI YONEDA[1]

ABSTRACT

Using larval specimens collected in bongo nets in southern Brazilian waters (between lat. 23° and 29°S), early development of the lophiid anglerfish, *Lophius gastrophysus*, is described and compared with other lophiid species. Larval morphology of *L. gastrophysus* is very similar to that of *L. americanus*, having three conspicuous melanophores on the trunk and caudal region, but the former can be easily distinguished from the latter by the presence of two melanophores on the preopercular and suborbital regions and positions of the melanophores on the elongate ventral fin.

The peculiar larvae of *Lophius* have been known since the description of the early developmental stage of *L. americanus* by Agassiz (1882). Their characteristic form with elongate dorsal and ventral fin rays makes them easily identifiable. Of the 25 species of the Lophiidae (Caruso 1981), larvae have been repeatedly described and discussed for *L. piscatorius* (Prince 1891; Williamson 1911; Stiasny 1911; Allen 1917; Lebour 1919, 1925; Bowman 1920; Tåning 1923; Arbault and Boutin 1968; Russel 1976) and for *L. americanus* (Agassiz 1882; Connolly 1920, 1922; Tåning 1923; Berrill 1929; Dahlgren 1928; Procter et al. 1928; Bigelow and Schroeder 1953; Martin and Drewry 1978; Fahay 1983; Pietsch 1984). The larvae of two other species also have been described: *L. budegassa* (Stiasny 1911; Padoa 1956) and *L. litulon* (Tanaka 1916; Mito 1966). There is no literature on larval morphology of *L. gastrophysus*.

During ichthyoplankton surveys along the southern Brazillian coast, many *Lophius* larvae were collected and identified as *L. gastrophysus*. This report gives a detailed comparative description of larval development based on 136 specimens collected during the past 13 years.

MATERIALS AND METHODS

Larval specimens used in this report were obtained from the collections of ichthyoplankton at the Instituto Oceanográfico da Universidade de São Paulo. These samples were collected from the southern Brazillian coast using a 61 cm bongo net following the sampling method of Matsuura (1979) and preserved in 10% Formalin[2] solution. Notochord length (NL) was taken from the tip of the upper jaw to the tip of the notochord. A total of 136 larvae (3.3-15.7 mm NL) of *L. gastrophysus* was used in this study. Specimens were measured with a micrometer in a stereoscopic dissecting microscope and illustrations were made with the aid of a camera lucida.

MORPHOLOGY OF LARVAE

The smallest identified specimens which were collected with plankton nets as free-living forms were about 3.3 mm NL, but they still had a large yolk sac. Fahay (1983) showed that the newly hatched larvae of *L. americanus* was as small as 2.5 mm long, and they were still encased in the egg veils (Fahay[3]). The reported size of newly hatched larvae of *L. piscatorius* was 4.5 mm TL (Lebour 1925).

Since the 3.3 mm larvae were not in perfect condition, we used larger specimens for the morphological description. Preflexion larvae of *L. gastrophysus* have a slender body (Fig. 1A, B, C, D), but they later become robust form (Fig. 1E, F). This change of body shape is partly a result of increase in body depth and partly due to enlargement of subepidermal space (Fig. 1C, D, E, F), which appears, firstly, on the head region and later becomes larger and extends posteriorly, giving the larvae a balloonlike appearance. This subepidermal space consists of transparent, gelatinous connective tissue and is considered an adaptation to planktonic life

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[2]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

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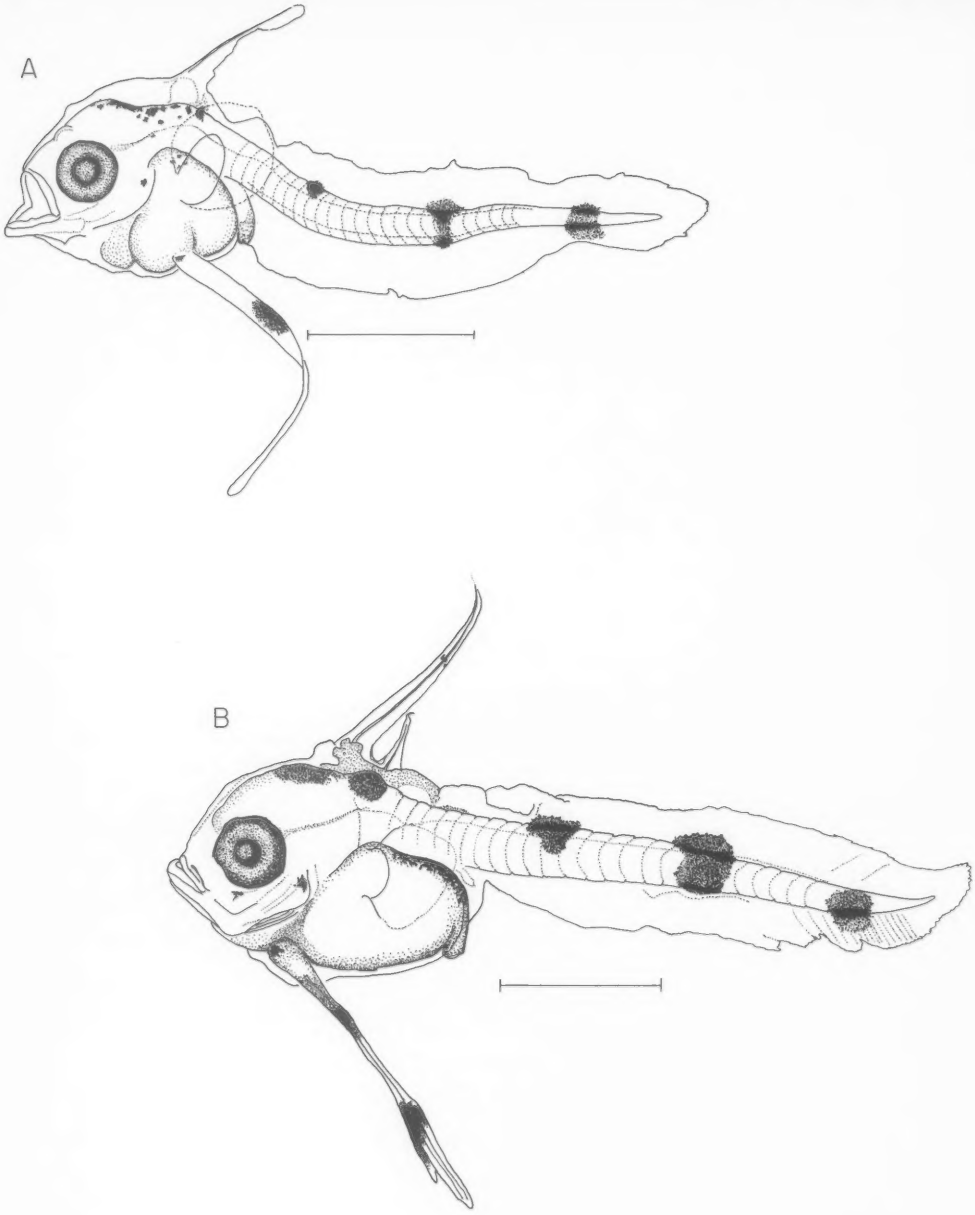

FIGURE 1.—*Lophius gastrophysus* larvae from southern Brazil: A. 3.8 mm NL, B. 4.5 mm NL. Scale bar is 1.0 mm.

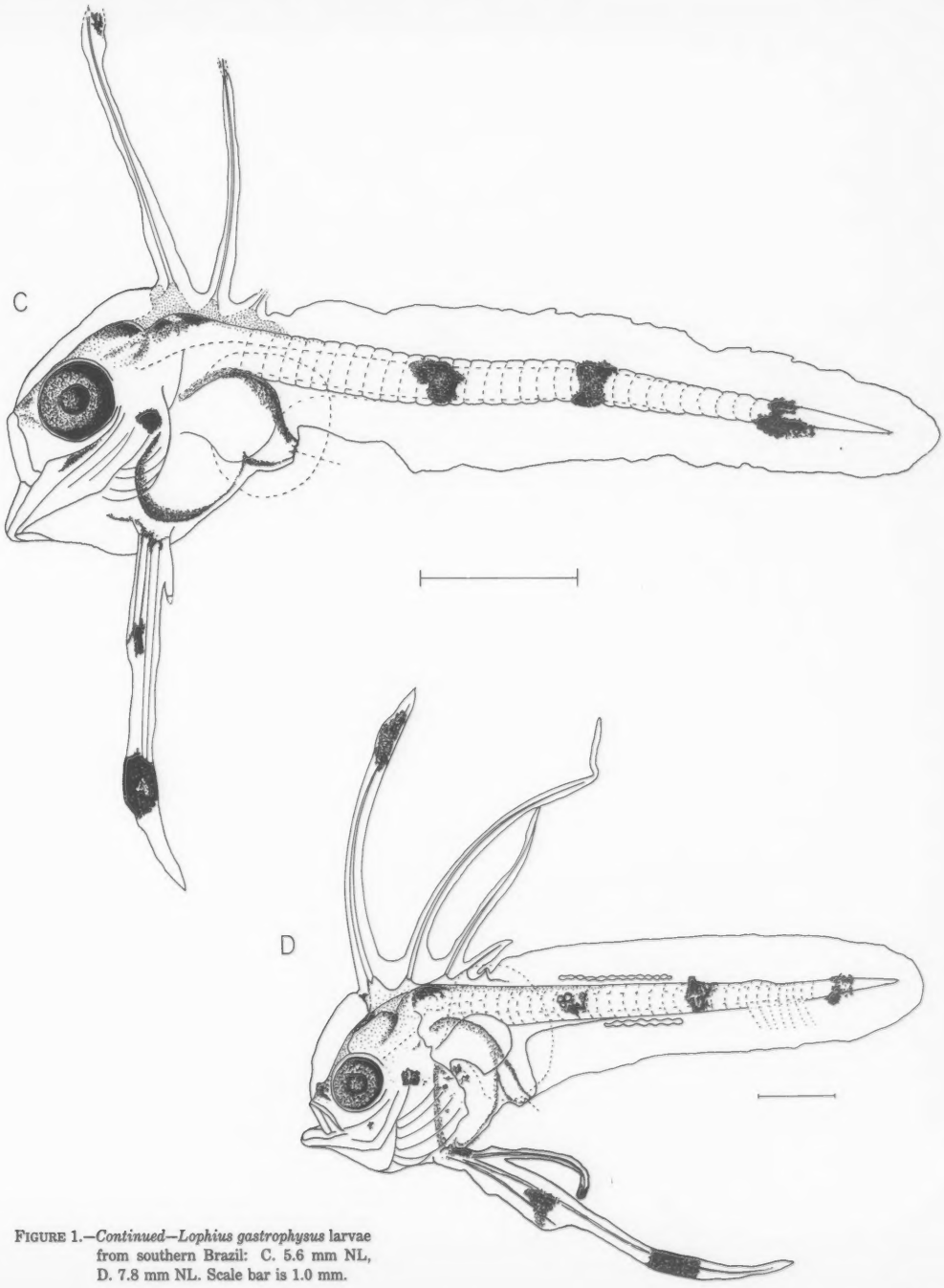

FIGURE 1.—*Continued—Lophius gastrophysus* larvae from southern Brazil: C. 5.6 mm NL, D. 7.8 mm NL. Scale bar is 1.0 mm.

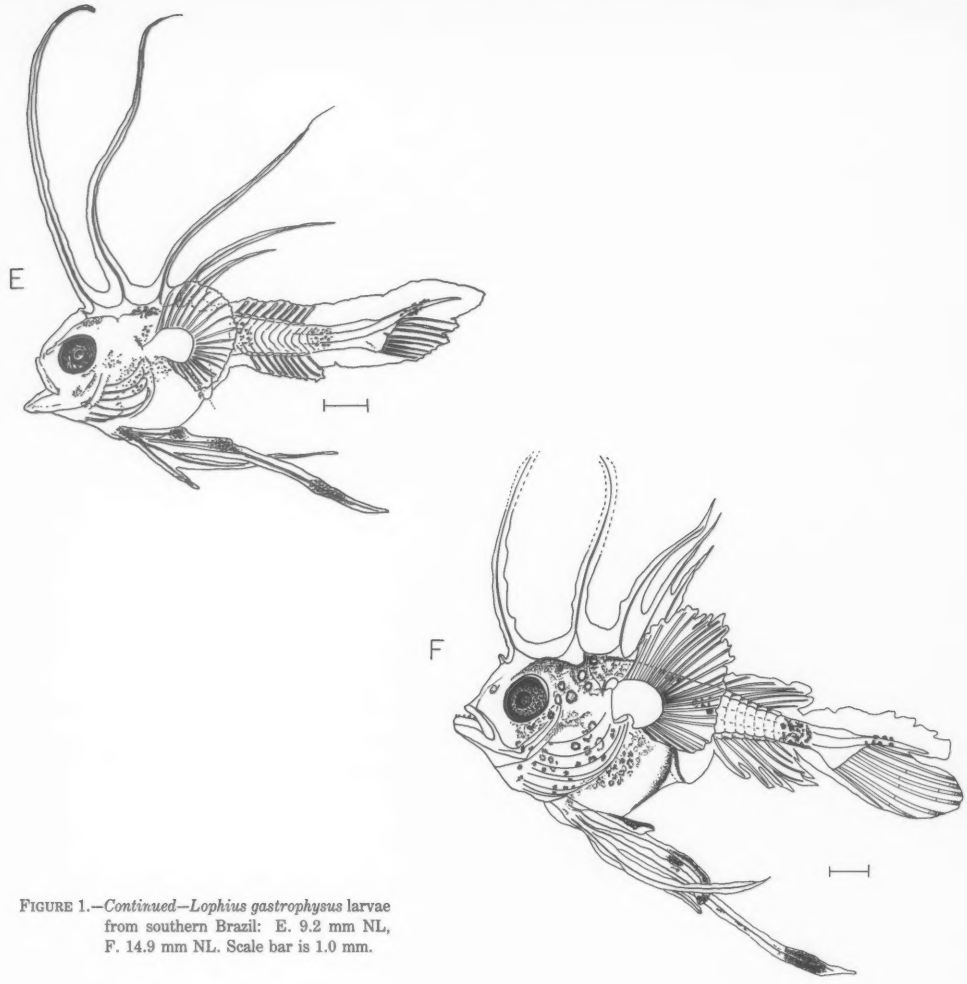

FIGURE 1.—*Continued—Lophius gastrophysus* larvae from southern Brazil: E. 9.2 mm NL, F. 14.9 mm NL. Scale bar is 1.0 mm.

(Tåning 1923). Notochord flexion starts at about 9 mm NL (Fig. 1E).

As shown in *L. piscatorius* larvae (Tåning 1923), the laterally compressed larval form changes gradually during their planktonic stage toward the dorsoventrally depressed shape of juvenile and adults. The largest larvae examined, 15.7 mm NL, had not yet achieved the juvenile stage, but a similar tendency was observed. For example, the maximal breadth of the head in 3.5 mm larva is only 22%, but that in 15.7 mm larva is about 40% of body length. The proportion of body depth also shows a similar tendency, i.e., it starts at 30% at 4 mm and attains 45% of body length at 15.7 mm. The proportion of head length starts at about 23% at 4.5 mm and attains almost 45% at 15.7 mm NL.

Statistics describing regressions of different body parts in relation to body length are shown in Table 1. The regressions lines of head length and body depth showed an inflexion at the size of 7.6 mm NL, while those of other body parts were linear for the size range 3.2-15.7 mm NL. Thus, the regressions

TABLE 1.—Statistics describing regressions relating notochord length with length of different body parts of *Lophius gastrophysus* larvae. *a* and *b* = constant ($y = a + bx$), *r* = correlation coefficient, *n* = number of specimens.

Characters (*x*)	Size range of notochord length (*y*) (mm)	*a*	*b*	*r*	*n*
Head length	3.2- 7.5	−0.18334	0.27117	0.68827	97
	7.7-15.7	−2.11501	0.56058	0.94483	27
Body depth	3.2- 7.5	0.10498	0.28333	0.74299	99
	7.7-15.7	−2.49286	0.65397	0.92825	27
Preanal distance	3.2-15.7	−1.54475	0.77254	0.96482	27
Predorsal distance	3.2-15.7	−1.65336	0.74641	0.96717	[illegible]
Eye diameter	3.2-15.7	−0.00095	0.10383	0.94353	124
Length of the second dorsal spine	3.2-15.7	−3.19397	0.99987	0.90707	96
Length of the third ventral fin ray	3.2-15.7	−3.47484	1.14083	0.90497	102

lines of the former were calculated in two size ranges.

PIGMENTATION

Lophius gastrophysus larvae develop a distinct pattern of melanophores. Since early stage (Fig. 1A), there are three large pigment bars on the trunk and caudal region and they remain at the same position during larval stage. The larva of 14.9 mm NL (Fig. 1F) has a heavily pigmented body, but the three large pigment bars on the trunk and caudal region are still visible. There are dense melanophores over the occipital region of the head and shoulder (Fig. 1A). Pigments on the elongate ventral fin ray is also visible in the smallest specimen, but the positions and number of them change gradually. In the earliest stage (3.8 mm NL) there are two melanophores on the ventral fin: one at the fin ray base and another at the middle of the ventral fin. At the size of 4.5 mm NL (Fig. 1B), there appears another small melanophore at one-third the length of the fin ray. The melanophore at the fin ray base remains at the same position, but the distal large one moves to the position three-fourths the length of the fin ray. After this size, positions and number of melanophores on the elongate third ventral fin ray remain the same up to 15.7 mm NL. When distal part of other ventral fin rays start to separate from the third one, there appears some melanophores on the distal edge of each fin ray.

There appears a patch of melanophores on the preopercular region at 3.8 mm NL and another small one appears on the suborbital region at 4.5 mm NL. The small melanophore, which appears on the tip of the elongate second dorsal spine at 4.5 mm NL, will later become a large pigment bar (Fig. 1C, D).

FIN DEVELOPMENT

The most remarkable change can be seen in lengths of the dorsal and ventral fins. Since the earliest stage (Fig. 1A), the larvae have elongate dorsal spine and ventral fin ray, which later become the second dorsal spine and the third ventral fin ray, respectively. The length of the second dorsal spine relative to body length changed from 28% at 3.3 mm NL to 90% at 8.3 mm NL (Fig. 2A). In larger larvae the proportion of the second dorsal spine length relative to body length decreased gradually to 70% at 15.7 mm NL. A similar tendency was observed for the length of the third ventral fin ray: it varied from 45% of body length at 3.3 mm NL to 121% at 11.6 mm NL (Fig. 2B). Unfortunately, these fin rays are in many cases lost or damaged at the distal tip, making it difficult to say whether we measured the total length of fin rays or the partial length of a damaged ray. In any case, the figure shows a clear tendency of rapid increase of fin rays during larval stage.

The number of fin rays increases during larval stage. For example, the origin of the first dorsal spine firstly appears anterior to the elongate second dorsal spine in 9.2 mm NL larva (Fig. 1E). The tip of the first dorsal spine which will transform into the illicium in the adult fish, emerges from the epidermal skin at about 10 mm NL. At this size, all fin rays are well developed and number of fin rays on the second dorsal, anal, and caudal fins attains the adult number.

Another remarkable change in fin development is a forward advancement of the dorsal spines. At 3.3 mm NL larva, the elongate second dorsal spine lies behind the head (Fig. 1A) and it moves gradually forward during larval stage; at 14.9 mm NL,

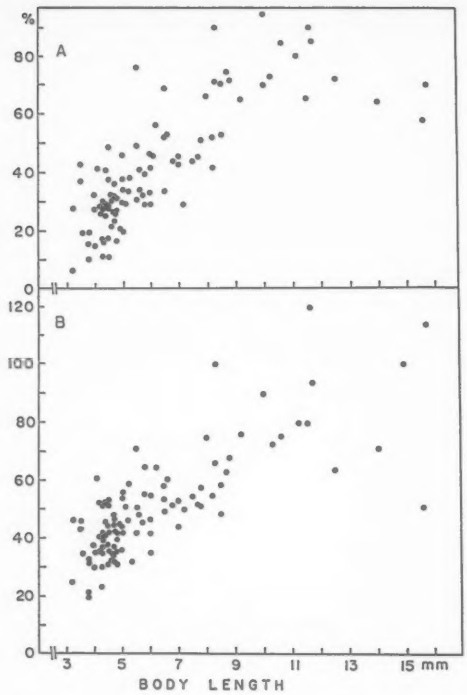

FIGURE 2.—Relationships between changes of proportion of second dorsal spine (A) and third ventral fin ray (B) and body length (NL) of *Lophius gastrophysus*.

it becomes the position anterior to the eyes (Fig. 1F).

DISCUSSION

Based on a study of world-wide collections, Caruso (1981, 1983) recently concluded that the Lophiidae is represented by 4 genera and 25 species, of which only 2 species inhabit the western Atlantic: *Lophius americanus* in the western North Atlantic and *L. gastrophysus* in the western Central and South Atlantic. The geographic ranges of the two species overlap between Cape Hatteras, NC, and Florida. The two western Atlantic species are very similar, but they can be easily distinguished by differences in dorsal and anal fin ray counts, size of the third and fourth dorsal spines, and differences in pigment pattern (Caruso 1983).

It is well known that lophiid anglerfishes spawn over deep water producing large gelatinous ribbons of spawn which often contain more than a million eggs (Berrill 1929). Spawning behavior is not known, but some authors have suggested that it may occur at or near the bottom (Tåning 1923; Dahlgren 1928). After hatching, the larvae emerge from the gelatinous capsules and pass a long planktonic stage. Upon attaining a length of about 60 mm TL, young fish probably take to the bottom (Connolly 1922; Tåning 1923; Bigelow and Schroeder 1953).

As shown previously, *Lophius* larvae can be easily distinguished from those of other species. Because there is only one species in the western South Atlantic, there is no doubt about the identification of our larvae as *L. gastrophysus*. Therefore, we have documented morphological differences in early developmental stages of our specimens and compared them with those of other well-known species (Table 2).

Meristic characters and adult forms of *L. americanus* and *L. piscatorius* are very similar, but their larval forms are quite different (Tåning 1923). The most remarkable difference is the presence of three large pigment bars on the trunk and caudal region in *L. americanus* from the yolk-sac stage. He also pointed out that the larval development of *L. americanus* was more rapid than that of *L. piscatorius*.

The larvae of *L. gastrophysus* are very similar to that of *L. americanus*. Both species have three large pigment bars on the trunk and caudal region from the very earliest stages. Larval development of *L. gastrophysus* is more rapid than that of *L. americanus*, e.g., formation of the bases of the second dorsal and anal fins and the five dorsal spines occurs at sizes 8.1 mm, 8.5 mm, and 11.5 mm, respectively, for *L. gastrophysus*, *L. americanus*, and *L. piscatorius*. In the same way, the first appearance of canine teeth on both jaws occurs at sizes of 4.2 mm, 6.5 mm, and 9.8 mm, respectively, in the same order for the three species.

Another difference is in the position of the melanophore of the ventral fin, present on the distal part of this fin in larvae of *L. americanus* and *L. piscatorius*, but at three-fourths the length of the fin in *L. gastrophysus* larvae. The presence of pigmentation in the preopercular and suborbital regions is also peculiar to *L. gastrophysus* larvae.

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TABLE 2.—Comparison of development stages of three Atlantic species of lophiid anglerfishes.

Characters	*L. gastrophysus*	*L. americanus*	*L. piscatorius*
General development			
Formation of bases of second dorsal and anal fins, the five dorsal spines, and the elongate ventral fin	8.1	8.5 mm[1]	11.5 mm[2]
First dorsal spine	about 10-11 mm	about 12-14 mm[1, 2]	about 15-16 mm[2, 3]
Completion of anal fin rays	9.3 mm	10.5 mm[2]	16 mm[3]
Completion of soft dorsal fin rays	9.3 mm	10.5 mm[2]	16 mm[3]
Size at first appearance of canine teeth in both jaws	4.2 mm	6.5 mm[2]	9.8 mm[2]
Size of newly hatched larva	about 3.5 mm	about 2.5 mm[4]	about 4.5 mm[3]
Pigment on distal edge of the second dorsal spine	since 5.2 mm	no pigment [1, 2]	since 6 mm[3, 5]
Position of pigment on distal part of the ventral fin	3/4 of ventral fin	far distal edge[2, 6]	far distal edge[5]
Pigment bars on the trunk and caudal region	three bars since early stage	three bars since[2] early stage	anterior two bars[5] since 11 mm
Meristic characters[7]			
Dorsal fin rays	9-11	11-12	11-12
Anal fin rays	8-9	9-10	9-10
Pectoral fin rays	22-26 (24.6)	25-28 (26.1)	23-27 (25.2)
Vertebrae	26-27 (26.2)	28-30 (29.1)	30-31 (30.4)

[1]Martin and Drewry 1978; [2]Tåning 1923; [3]Russel 1976; [4]Fahay 1983; [5]Lebour 1925; [6]Agassiz 1882; [7]Caruso 1983.
Note: For comparative purpose, the body length was given in total length for all species. Notochord length of *L. gastrophysus* larvae was converted to total length with an equation: TL = 1.024 mm NL + 0.1168 (r = 0.999), for larvae smaller than 10.0 mm NL.

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EX-VESSEL PRICE LINKAGES IN THE NEW ENGLAND FISHING INDUSTRY

DALE SQUIRES[1]

ABSTRACT

This study examines the direction of ex-vessel price linkages between the three New England ports of Boston, New Bedford, and Gloucester. Within-sample, bivariate tests of Granger causality are applied for monthly data from 1965 through 1981. It is found that cod and haddock prices are formed in New Bedford, that pollock prices are simultaneously formed between Boston and Gloucester, and that a spurious relationship exists for flounder prices between the three ports. The hypothesis is advanced that this spurious relationship may be due to flounder price leadership from outside the region, most probably the New York Fulton Fish Market.

The direction of price linkages between various market and production centers in an industry is important to studies of marketing and prices. Although these spatial and hierarchical relationships are generally well understood in domestic agriculture, they have received little or no attention in natural resource utilization and in the domestic commercial fishing industry in particular. This study therefore examines the spatial characteristics of round ex-vessel price linkages of the most important species in the New England fishing industry from 1965 through 1981.

Three ports—New Bedford, Boston, and Gloucester—dominate the New England fishing industry, as both home ports or production centers and as marketing centers. By both volume and value of landings, New Bedford is the most important port, followed by Gloucester and then Boston. The most important species of groundfish in New England are cod; haddock; yellowtail, winter, and other flounders; ocean perch or red fish; and pollock. Sea scallops and lobsters also provide a significant contribution to the industry in both value and volume of landings. This study accordingly focuses upon the ports of Boston, New Bedford, and Gloucester, and the species of cod, haddock, yellowtail and winter flounders, and pollock. Additional attention is given to ocean perch and sea scallops, though rigorous conclusions are not possible.

In New Bedford and Boston, fishermen sell their catches to the highest bidder in an open auction. The New Bedford auction begins at 8:00 a.m. and ends at 8:22 a.m. The Boston market begins at 7:00 a.m., and invariably overlaps with the New Bedford market. There is significant communication between the two markets during the auctions. The volume and total value of fish harvested is substantially greater in New Bedford than in Boston. Bidders purchase an entire vessel's landings in New Bedford, while in contrast, purchasers offer individual bids for each species in Boston. In most of the ports other than Point Judith in Rhode Island (where an important fishermen's cooperative exists), the catch is sold directly to fish processors or by prior arrangements between individual vessels and purchasers. Further, it is generally believed that Gloucester prices for most fresh groundfish species are set in Boston, and differ only by a transportation cost.

Fishermen of all ports are free to land their harvests at any port offering the highest prices, which, however, must be balanced against steaming time. Few vessels land exclusively at a single port, since the distances between the three are not great. A definite limit exists to port switching due to the prevalence of market transactions costs. Wilson (1980) indicated that personal and financial relationships tend to bind particular fishermen and fish buyers. In contrast to many other natural resource and primary production industries, a futures market does not exist for fresh fish.[2]

Different ports and markets have developed singular reputations. These specializations are based in large part upon proximity to resource stocks. New Bedford has developed a reputation as a flounder and sea scallop port, while Boston has become known as a cod, haddock, and, to a lesser extent,

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[2]Trading on futures markets involves buying and selling standardized contracts for the future delivery of a specific grade of a commodity at a specific location(s).

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pollock port. Although Gloucester fishermen direct much of their effort towards cod, haddock, and flounders (generally joint products), Gloucester has developed a reputation as a port for both pollock and ocean perch.

Conventional wisdom in the New England groundfishery market holds that New England round (fish as harvested) ex-vessel prices of fresh flounders are formed in the New Bedford auction market, while fresh cod, haddock, and pollock round ex-vessel prices are set in the Boston auction. These widely held beliefs serve as the null hypotheses to be tested in this study of the ex-vessel groundfish price linkages in New Bedford, Gloucester, and Boston.

Knowledge of ex-vessel price linkages has a number of applications. Efforts at improving market efficiency would find this information useful. The broadcasting of daily ex-vessel fish prices by the National Marine Fisheries Service can properly focus upon the most crucial markets. Infrastructural or institutional improvements can be more judiciously targeted, an important consideration in a time of tight public and private budgets. Price forecasts to improve industry functioning can concentrate upon those prices formed in markets which demonstrate price leadership. Fishermen may want to land their harvests in the market in which ex-vessel prices are first formed, should fishermen want to affect the pricing process, be less dependent upon the landings of others, or capture advantageous prices. Similar considerations apply to buyers. Knowledge of the price formation process allows government price policies to target the appropriate markets. Finally, price linkage information is crucial to studies of marketing margins, length of price transmission, and asymmetric pricing.

THE DATA

The data are taken from the vessel weighout files of the National Marine Fisheries Service. After every trip of a commercial fishing vessel of any gear type, port agents in each port obtain the value and volume of landings for each species harvested. The entire collection of this information constitutes the weighout file. The output vector from the weighout file is then linearly aggregated over vessels and trips to form monthly round ex-vessel prices for each port. The resulting nominal prices are subsequently deflated by the consumer price index for food. As Sims (1974) and Feige and Pierce (1980) noted, the use of seasonally adjusted data may confound lag distributions and causality relationships. Consequently, the data are left in their unseasonalized state. However, to account for seasonal differences, quarterly dummy variables are employed. The time domain of the data set extends from 1965 through 1981.

METHOD OF ANALYSIS

Granger (1977) provided a definition of causality among a set of variables that is based upon predictability as well as the fact that the effect of a change in an exogeneous variable upon an endogeneous variable requires time. A variable X causes another variable Y, with respect to a given universe or information set that includes X and Y, if present Y can be better predicted by using past values of X than not doing so, all other information in the past of the universe being used in either case. Causality from Y and X is defined in the same manner. Feedback occurs if X causes Y and Y causes X. A causal relationship between X and Y does not exist if causality does not run from X to Y or from Y to X, and feedback does not occur.

Causality tests may be classified into two fundamental types at their most basic level, within-sample and out-of-sample tests. The within-sample test is widely applied and is the first one developed. This test is developed over the full-time domain of the data set, and essentially relies upon a measure of fit. The definition of causality in the out-of-sample test requires evidence of improved forecasts. This approach is implemented by identifying and estimating different models using the first part of the sample and then comparing their respective forecasting abilities on the latter part of the sample. This study utilizes the within-sample test, the one most commonly applied, since the properties of the out-of-sample test have yet to be systematically examined.

Two basic approaches have been advanced by which to apply empirically the within-sample bivariate Granger criterion to time series. The first approach is represented by the test proposed by Pierce (1977) based upon Haugh (1976). The procedure first estimates whitening filters for each time series, then subsequently estimates the cross-correlation function for the first step's residuals.[3] However, Sims (1977) and Geweke (1981) indicated that this approach may be limited.[4] A second basic

[3]Whitening filters remove serial correlation from a time series. Each time series used in a test of causality will be a white noise process, and any relationships will be based on actual, systematic relationships between the two time series, instead of a spurious relationship caused by the common serial correlation.

[4]Prefiltering each time series with separate autoregressive integrated moving average (ARIMA) filters biases the test toward

approach relying directly upon distributed lag relationships between dependent and independent variables has led to three widely used tests: those suggested by Sims (1977), the direct Granger test forwarded by Sargent (1976), and the Modified Sims test advanced by Geweke et al. (1983).

The small-sample properties of the Sims (1972), direct Granger, and Modified Sims tests have recently been examined within Monte-Carlo frameworks by Guilkey and Salemi (1982) and Geweke et al. (1983). Although the two studies differ somewhat in their specifications, both found that the Sims test was outperformed by the other two. Since the Sims test is more time-consuming and expensive to employ and requires more decisions about parameterizations, both studies unequivocally recommend against its use.

The two studies reach slightly different conclusions on the efficacy of the direct Granger and Modified Sims test. These contradictory results can be attributed to differences in research design. Geweke et al. (1983) concluded that the two tests essentially perform equally well. In contrast, Guilkey and Salemi (1982) determined that the direct Granger test consistently outperforms the Modified Sims procedures by small amounts. Since the direct Granger test is computationally the least expensive of the three and results in the fewest degrees of freedom lost from formation of leads and lags, Guilkey and Salemi recommend its use over the Modified Sims and Sims procedures. Nonetheless, they do note that the Granger procedure's advantage over the other two diminishes with increases in sample size.

Several additional findings of Guilkey and Salemi (1982) are also worth reporting. They observed that for sample size <200, the shorter versions of all three tests are superior to the longer versions.[5] They further noted that in their Monte-Carlo study the direct Granger and Modified Sims procedures accurately recover the coefficients of the relevant population projections of the statistical model used to generate experimental time series in small samples. Consequently, it may be unlikely to observe "large" coefficient estimates arising spuriously. Finally, test performance is extremely sensitive to sample size, strength of causation, and length of test parameterization employed.

The direct Granger test as applied in this study is based upon ordinary least squares regression of the current observation of the time series of round ex-vessel prices from one port upon its own past observations and the past observations of the other port's round ex-vessel prices for species k:

$$P2_k(t) = a_k + \sum_{i=2}^{4} b_{ki} D_i + cLT + \sum_{j=1}^{J} d_{kj} P2_k \times (t-j) + \sum_{j=1}^{J} f_{kj} P1_k (t-j) + e_{kt}. \quad (1)$$

Here, LT refers to a linear time trend, D_i is the zero-one variable for quarter i, $P1_k(t)$ is the round ex-vessel price of species k in month t in port 1, J is the number of periods lagged, and e_{kt} is a vector of stochastic, white noise residuals. The presence of lagged dependent variables in Equation (1) is counted on to remove serial correlation from the estimated residuals.[6]

The test of the null hypothesis that $P1_k$ does not cause $P2_k$ is a test that $f_{kj} = 0$, $j = 1,2,\ldots,J$. Guilkey and Salemi (1982) indicated that the F-test statistic is calculated by estimating Equation (1) in both constrained ($f_{kj} = 0$, $j = 1,2,\ldots,J$) and unconstrained forms, and may be written as[7]

$$F = \frac{(SSE_c - SSE_u)/J}{SSE_u/(T - (2J + 2))}, \quad (2)$$

where SSE_u and SSE_c are the residual sum of squares from the unconstrained and constrained regressions, respectively, and T represents the number of monthly observations on round ex-vessel prices. Under the null hypothesis, F is an F-test statistic with J and $T - (2J + 2)$ degrees of freedom. This procedure is then repeated reversing the roles of $P1_k$ and $P2_k$ to test the null hypothesis that $P1_k$ does not cause $P2_k$.

The direct Granger test requires selection of a lag length, J, large enough to purge serial correlation from estimated residuals. Several factors require consideration before specifying the lag length. Chilled fresh fish is a commodity that rapidly deteriorates in quality. Consequently, definite limits exist to the length of time which inventories of

failing to reject the null hypothesis of independence of the two series more often than the specified level of significance suggests. Because of this limitation, the second basic approach is applied.

[5]Longer versions of these tests include additional lead and lag variables.

[6]Serial correlation exists when the error terms from different observations in a time series are correlated. Serial correlation tends to give unbiased but inefficient estimators, and a biased sampling variance, which then affects the results from significant tests such as the F- or -t-tests.

[7]A constrained F-test includes one or more restrictions, such as one or more coefficients constrained to zero. An unconstrained F-test does not include these restrictions.

chilled fresh fish can be held. Since most groundfish harvested in New England waters are not processed into frozen fish products, long-term storage of New England groundfish is unlikely, and fresh fish prices are likely to adjust more quickly than those of most other food commodities. In addition, previous exploratory analysis with adaptiver filtering methods on the weighout file suggests that two sets of round ex-vessel prices for any species k are particularly important, the previous month's price and the price within one month on either side of the previous year. In order to account for these characteristics and to provide both short and long versions of the test, lags of 8 and 14 mo were specified. These lag lengths are sufficiently long to encompass price lags with monthly data. The diagnostic Q test of Box and Pierce (1970) is used to detect serious serial correlation.

EMPIRICAL RESULTS

The empirical results from the direct Granger causality tests lead to somewhat unexpected conclusions for most species. The null hypothesis that monthly round ex-vessel prices of cod and haddock in all three ports are first formed in the Boston auction market is rejected in almost all instances. The findings in Table 1 instead suggest that the cod and haddock prices established in the New Bedford auction lead the prices formed in the Boston market. Several factors may account for this. The New Bedford auction's volume of landings is substantially higher than that of Boston. In addition, the two market times ordinarily overlap, and frequent communication occurs between economic agents during the auctions. Further, the proximity of New Bedford to Boston allows fresh fish to be easily trucked to Boston from New Bedford. The markets are thus physically linked, before the auctions by fishermen and after the auctions by fish buyers. One element of conventional wisdom may perhaps be substantiated, however. Although the Q-test statistic indicates severe serial correlation (and thereby possibly refuting the F-test statistic), the empirical results indicate that Boston cod prices do lead Gloucester cod prices at the ex-vessel level for the shorter lag length parameterization.

Rejection of the null hypothesis that Boston prices lead New Bedford and probably Gloucester cod and haddock round ex-vessel prices and the finding that New Bedford prices lead Boston prices suggest a second null hypothesis for consideration. This second hypothesis states that Gloucester cod and haddock prices are directly led by New Bedford prices. In addition, the possibilities that Boston prices lead Gloucester prices and that New Bedford prices lead Boston prices suggest an additional, indirect price linkage between Gloucester and New Bedford via Boston.

The results for this second null hypothesis are also given in Table 1. Since this is an unplanned comparison, a Scheffe interval is used.[8] Strictly followed,

[8]An unplanned comparison occurs when in the course of examining results a hypothesis is tested which was not specified prior to the experiment. The initial region is altered by the additional information, so that the level of significance has changed. A Scheffe interval allows for a more cautious test by providing a larger critical value than that given by a t or F table. This pre-test bias is accounted for by a conservative test. The F-test statistic now

TABLE 1.—Direct Granger causality tests for monthly fresh round ex-vessel cod and haddock prices.

Cod				Haddock			
Direction[1]	Lags[2]	F-test[3]	Q-test[4]	Direction[1]	Lags[2]	F-test[3]	Q-test[4]
B ------->G	8	2-37*	35.67*	B ------->G	8	1.69	9.60
B ------->G	14	1.17	2.61	B ------->G	14	1.09	4.49
G ------->B	8	1.59	10.98	G ------->B	8	1.07	10.98
G ------->B	14	1.02	12.35	G ------->B	14	1.29	15.07
B ------->NB	8	1.67	13.52	B ------->NB	8	0.08	12.54
B ------->NB	14	0.74	21.85*	B ------->NB	14	0.09	7.06
NB ------->B	8	2.52*	8.82	NB ------->B	8	3.15*	8.62
NB ------->B	14	1.89*	16.27	NB ------->B	14	1.76*	8.74
G ------->NB	8	1.78	16.46	G ------->NB	8	0.56	11.71
G ------->NB	14	0.91	28.42	G ------->NB	14	1.36	15.09
NB ------->G	8	[5]2.96	7.84	NB ------->G	8	[5]2.90	11.76
NB ------->G	14	1.40	6.86	NB ------->G	14	1.65	8.37

[1]Variable abbreviations are B (Boston), G (Gloucester), NB (New Bedford).
[2]J indicates J months lagged.
[3]Null hypothesis that past values of the causal variable do not significantly affect current values of the dependent variable. An asterisk indicates rejection of the null hypothesis at the 5% level.
[4]Null hypothesis that regression residuals are white noise. An asterisk indicates rejection of the null hypothesis at the 5% level.
[5]F-test statistic is significant at the 5% level, but not significant at the 5% level when a Scheffe interval is used.

the results indicate that the cod and haddock price linkage does not run from New Bedford to Gloucester. If a Scheffe interval is not used, then the New Bedford cod and haddock prices do lead those of Gloucester. Therefore, with this caveat, New Bedford auction market monthly round ex-vessel cod and haddock prices lead the prices of Gloucester and Boston, and Boston prices may lead those of Gloucester. In any case, it appears that the New Bedford auction market dominates the formation of round ex-vessel prices for cod and haddock.

The empirical results for yellowtail and winter flounder of Table 2 also contradict the null hypothesis that monthly fresh round ex-vessel prices for both species are formed first in New Bedford. Instead, the findings indicate that pricing feedback exists between both New Bedford and Gloucester and between New Bedford and Boston. These conclusions must be tempered by the significant Q-test statistics for several relationships.

These conclusions lead to a second null hypothesis to be tested on the yellowtail and winter flounder price linkages between Gloucester and Boston. Since this test is also an unplanned comparison, a Scheffe interval is required. Again, the strict test results indicate that neither port's prices lead the other, nor that feedback exists.

The most probable explanation for the feedback between the prices of New Bedford and Gloucester, New Bedford and Boston, and possibly between Gloucester and Boston rests with a spurious relationship. Although New Bedford is the most important flounder port by landings in New England, New York City is even more important on the eastern seaboard by volume of consumption. New York City's Fulton Fish Market is primarily a wholesale market without substantial landings. Much of the New England flounder harvested is sent to Fulton on consignment without an ex-vessel price being established in New England. The Fulton Fish Market also begins much earlier in the morning than New Bedford's auction market. Thus the apparent feedback among the ex-vessel yellowtail and winter flounder prices in the New England ports is probably due to their following of the wholesale prices set in the Fulton Fish Market.

Table 3 presents the results for pollock. As with the other species, consistent results are obtained for different lag lengths. Again, the null hypothesis dic-

TABLE 2.—Direct Granger causality tests for monthly fresh round ex-vessel yellowtail and winter flounder prices.

Yellowtail flounder				Winter flounder			
Direction[1]	Lags[2]	F-test[3]	Q-test[4]	Direction[1]	Lags[2]	F-test[3]	Q-test[4]
NB ——>G	8	2.05*	20.19	NB ——>G	8	7.52*	5.68
NB ——>G	14	2.27*	19.42	NB ——>G	14	8.71*	1.78
G ——>NB	8	1.96*	23.56*	G ——>NB	8	2.88*	16.98
G ——>NB	14	2.48*	26.78*	G ——>NB	14	2.97*	22.19*
NB ——>B	8	2.02*	10.56	NB ——>B	8	11.87*	18.45
NB ——>B	14	1.76*	9.89	NB ——>B	14	7.66*	7.92
B ——>NB	8	0.75	17.63	B ——>NB	8	23.57*	9.94
B ——>NB	14	2.83	21.83*	B ——>NB	14	5.25*	3.99
G ——>B	8	2.27[5]	9.41	G ——>B	8	3.87[5]	12.43
G ——>B	14	2.50[5]	12.74	G ——>B	14	4.37[5]	4.70
B ——>G	8	1.48	16.86	B ——>G	8	4.15[5]	18.16
B ——>G	14	1.27	18.82	B ——>G	14	3.56[5]	17.34

[1]Variable abbreviations are B (Boston), G (Gloucester), NB (New Bedford).
[2]J indicates J months lagged.
[3]Null hypothesis that past values of the causal variable do not significantly affect current values of the dependent variable. An asterisk indicates rejection of the null hypothesis at the 5% level.
[4]Null hypothesis that regression residuals are white noise. An asterisk indicates rejection of the null hypothesis at the 5% level.
[5]F-test statistic is significant at the 5% level, but not significant at the 5% level when a Scheffe interval is used.

TABLE 3.—Direct Granger causality tests for monthly fresh round ex-vessel pollock prices.

Direction[1]	Lags[2]	F-test[3]	Q-test[4]
B ——>G	8	4.34*	12.54
B ——>G	14	4.99*	10.15
G ——>B	8	5.28*	18.27
G ——>B	14	4.77*	22.96*

[1]Variable abbreviations are B (Boston), G (Gloucester), NB (New Bedford).
[2]J indicates J months lagged.
[3]Null hypothesis is that past values of the causal variable do not significantly affect current values of the dependent variable. An asterisk indicates rejection of the null hypothesis at the 5% level.
[4]Null hypothesis that regression residuals are white noise. An asterisk indicates rejection of the null hypothesis at the 5% level.

becomes significant only if it exceeds in magnitude $((a\text{-}1)F_b)^{1/2}$, where F is the $b \cdot 100\%$ critical value for F (a-1, N-a) and N is the number of observations. See Snedecor and Cochran (1976, p. 271) for more details.

tated by widely held industrial perceptions is rejected. The results indicate that feedback exists between the monthly fresh round ex-vessel prices of pollock in both Gloucester and Boston. Both ports dominate pollock landings and are close to one another.

A complete time series of prices for sea scallops exists only for New Bedford. Since New Bedford greatly dominates this fishery by both volume and value of landings, it may be safely concluded that monthly round ex-vessel sea scallop prices are formed in New Bedford. Finally, Gloucester is the only one of these ports to possess a complete time series of prices and landings of ocean perch or red fish. Since Gloucester dominates this fishery, monthly fresh round ex-vessel ocean perch prices appear to be formed in this port, at least among these three.

CONCLUDING COMMENTS

The within-sample bivariate direct Granger causality tests of monthly round ex-vessel price linkages for the three most important New England ports (Boston, New Bedford, and Gloucester) and the most important groundfish species lead to unexpected results. Conventional wisdom considers the round ex-vessel cod and haddock prices formed in the Boston auction market to lead the comparable prices of the other New England ports. However, the empirical results indicate that New Bedford's prices lead those of the other ports, although in certain cases Boston's cod prices may lead those of Gloucester as well.

The common industry perception also holds that the yellowtail and winter flounder round ex-vessel prices are first formed in New Bedford and lead those of Boston and Gloucester. Instead, the empirical findings suggest that feedback and simultaneous price formation occur among all three ports for both species. Since flounder landings in Boston and Gloucester are negligible in comparison to those of New Bedford, a spurious relationship due to the leading wholesale prices formed in the even earlier and more flounder-important Fulton Fish Market of New York City is suggested. Feedback is likely for fresh round pollock ex-vessel price formation in Boston and Gloucester. Finally, it is suggested that the New Bedford auction market dominates fresh ex-vessel sea scallop price formation and that Gloucester dominates among these three ports for ocean perch. New Bedford thus generally dominates ex-vessel price formation among the major New England ports for the most important species harvested.

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COMMUNITY STUDIES IN SEAGRASS MEADOWS: A COMPARISON OF TWO METHODS FOR SAMPLING MACROINVERTEBRATES AND FISHES[1]

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ABSTRACT

The effectiveness of using an otter trawl for estimating macrofaunal species ranks and abundances in seagrass meadows is unknown. In this study, we compare the catch effectiveness of the commonly used 5 m otter trawl with that of a 0.9 m wide epibenthic crab scrape for fishes, decapod crustaceans, molluscs, and echinoderms, using data from both day and night collections from a northeast Gulf of Mexico seagrass meadow. The crab scrape collected significantly more individuals and species of all taxa except (water-column) fishes. Clear discrepancies existed between trawl and scrape estimates of species ranks and relative abundances, with trawl collections estimating a higher degree of dominance within groups of shrimps and demersal fishes, and lower dominance among crabs. Whereas the crab scrape was clearly superior to the trawl for sampling macroinvertebrates and demersal fishes, the trawl was the better device for collecting water-column fishes. Explanations for observed differences in the sampling effectiveness of these gears are discussed. Sampling was considerably more productive at night than during the day. The combined approach of day-night sampling with both a crab scrape (for demersal fishes and epibenthic invertebrates) and an otter trawl (for water-column fishes) is recommended for community-wide studies in seagrass meadows.

Hypotheses concerning ecological community dynamics should be based upon accurate descriptions of the habitats and species involved. It is thus essential that collection methods maximize sampling efficiency in "community" (sensu Pielou 1977) studies. Because estimates of species composition, relative abundances, and biomass in aquatic environments may vary with different sampling devices (e.g., Lewis and Stoner 1981; Stoner et al. 1983), knowledge of sample gear effectiveness allows a more rigorous approach to sampling design and interpretation of results from studies of aquatic communities.

Seagrass community studies often employ a small, semiballoon otter trawl (try net) for sampling fishes and epibenthic invertebrates (Kikuchi 1966; Livingston 1975, 1976, 1982; Heck 1976, 1977, 1979; Hooks et al. 1976; Heck and Wetstone 1977; Weinstein and Heck 1979; Heck and Orth 1980; Orth and Heck 1980; Ryan 1981; Dugan and Livingston 1982; Dugan 1983). Although a small otter trawl may be one of the most effective samplers for estimating relative abundances of juvenile and small pelagic fishes in shallow nonvegetated waters (Kjelson and Johnson 1978; Orth and Heck 1980), there are few published accounts of its effectiveness in sampling benthic fishes or epibenthic invertebrates in vegetated habitats. Greening and Livingston (1982) noted that a Chesapeake Bay crab scrape appeared to collect more invertebrate species per sample effort in vegetated habitats than did an otter trawl. Miller et al. (1980) found a crab scrape to be more effective than either an otter trawl or a push net for collecting juvenile blue crabs, *Callinectes sapidus*, in the Chesapeake Bay area. Blue crab fishermen routinely use crab scrapes, rather than trawls, in grassbeds in Chesapeake Bay (Warner 1976).

In this study, the catch effectiveness of a 5 m otter trawl is compared with that of a 0.9 m epibenthic scrape in the shallow grassbeds of Apalachee Bay, FL. Species richness and abundance are examined within four taxonomic groups (decapod crustaceans, molluscs, echinoderms, and fishes). Because many grassbed organisms are more susceptible at night to certain sampling methods (Ryan 1981; Greening and Livingston 1982), both day and night samples are considered.

METHODS

Day and night samples were taken in about 1.7 m of water from seagrass beds in Apalachee Bay, FL.

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The sample site was located 5 km southwest of the Econfina River mouth (permanent station E-12 (Livingston 1975)). This site is characterized by relatively uniform, dense stands of the seagrasses, *Thalassia testudinum* and *Syringodium filiforme*, with seasonal occurrence of red drift algae (mean annual macrophyte biomass = 320 g dry wt/m^2; see Zimmerman and Livingston 1979 for a description of macrophytes). Station E-12 was polyhaline, with salinities during collections ranging from 22 to 30 ppt ($\bar{x}$ = 27.0 ppt). Water temperatures ranged from 12.0° to 31.0°C ($\bar{x}$ = 19.9°). Depth varied from 1.6 to 2.1 m. Physical characteristics are summarized in Table 1.

TABLE 1.—Physical characteristics of the sampling station for collection dates, Apalachee Bay, FL.

	Temp. (°C)	Salinity (ppt)	Depth (m)
Jan. 1979			
Day	12	31	2.0
Night	10	30	1.8
Apr. 1979			
Day	22	23	2.1
Night	21	22	1.6
July 1979			
Day	31	25	1.7
Night	30	25	2.1
Oct. 1979			
Day	17	30	2.1
Night	16	30	1.7

A 90 cm wide commercial Chesapeake Bay crab scrape (Miller et al. 1980) was fitted with the cod end of a 5 m otter trawl (6 mm mesh liner). The crab scrape was towed at about 1.4 knots for 1 min (after Greening and Livingston 1982; Leber 1983), yielding a standardized tow of 42 m (mean of 10 preliminary measured 1-min tows). A 42 m weighted line was then used to standardize scrape tows during collections. A 5 m otter trawl (19 mm mesh wings, 6 mm mesh liner in the cod end) was towed at the same speed for 2 min (as in Livingston 1975, 1982; Hooks et al. 1976; Heck 1977, 1979; Orth and Heck 1980; Stoner 1980; Stoner and Livingston 1980; Dugan and Livingston 1982; Dugan 1983), covering an average measured distance of 84 m. Under tow, the trawl mouth tickler chain fished a 2.1 m wide path over the substratum (Leber, pers. obs.). Hence, each individual trawl tow fished over 4.6 times the substratum surface area sampled by each tow of the crab scrape (176 m^2 vs. 38 m^2). Because the scrape collected larger amounts of dead vegetation, it was logistically difficult to sample as much surface area with it as was sampled by the trawl.

Collections were made quarterly (January, April, July, and October). On each sampling date eight scrape and four trawl tows were taken (in the sequence two trawls, eight scrapes, two trawls) during the day, and again beginning 1 h after dark. Greening and Livingston (1982) determined that eight 1-min scrapes were sufficient for sampling >95% of the species of macroinvertebrates at our sample site in Apalachee Bay. Because each scrape was towed for only half the 2-min towing time used for each trawl (scrape tows lasting longer than 1 min often resulted in clogging the net with red drift algae), only four trawls were taken during each sampling period. Thus, the combined length of the eight scrape tows (8 × 42 m = 336 m) matched that of the four trawl tows. All samples were collected from a 0.25 km^2 area immediately south of the station marker. Replicate tows were taken along transects spaced at least 30 m apart to prevent overlapping samples.

Organisms were preserved in 10% Formalin[4] (buffered with seawater) in the field, then identified, counted, and measured in the laboratory. A two-way, Model II, factorial ANOVA design for unequal but proportional cell sizes (Sokal and Rohlf 1969) was used to compare mean numbers of species and individuals of each taxon group in scrape vs. trawl (Factor 1) and day vs. night (Factor 2) samples. Log_{10} transformations were used where F-max tests indicated heterogeneity of variance. Rather than extrapolating our data to numbers per unit area, we compared the collections made with these two gears using absolute numbers per tow in our calculations (which are biased in favor of the trawl by a factor of 4.6). We used these absolute abundances because 1) we wanted a strongly conservative test of our premise that the scrape is the more effective of these two sample gears in vegetated aquatic habitats, and 2) we believe that extrapolations of semiquantitative data to abundances per unit area yield highly unrealistic results, which may be misinterpreted by readers as accurate densities (cf. Howard 1984, who determined that a towed beam trawl was only 4.7% efficient in estimating densities of shrimp in an Australian seagrass meadow).

RESULTS

Factor 1: Trawl vs. Scrape

Although the surface area sampled by the otter

[4]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

trawl during each tow exceeded that sampled with the crab scrape by a factor of 4.6, mean numbers of individuals collected in scrape samples were significantly greater than those in trawl samples in 44% of the 16 scrape-trawl comparisons (Table 2). The trawl was a significantly more effective collecting device for number of individuals of fishes (Table 2; April, July, and October fishes), but interaction terms were significant for April and October analyses (see Interactions, below). Mean numbers of individuals were greater in trawl, than in scrape, samples in two other cases (Fig. 1, January and July decapods in night samples); however, scrape-trawl differences on those dates were nonsignificant (Table 2). The crab scrape was clearly the better gear for sampling epibenthic individuals.

Species numbers were never significantly greater in trawl, than in scrape, samples (Fig. 1). In contrast, the crab scrape collected significantly more species than the trawl in 75% of the scrape-trawl comparisons (Table 2). Because the scrape often sampled greater numbers of individuals than the trawl, the presence of more species in scrape, than in trawl, samples may be simply a sampling phenomenon. By chance alone, one would expect to encounter more rare species in larger samples. Using rarefaction analysis (Simberloff 1978), we have factored out the influence of sample size on species number for a better comparison of scrape vs. trawl sampling effectiveness (Fig. 2). Eight of the 12 cases in which the scrape sampled significantly more species than the trawl (Table 2) can be attributed to a sampling phenomenon; there were generally more species in scrape samples because so many more individuals were collected in each scrape tow. However, it is clear in Figure 2 that the greater numbers of decapod species in January and July scrape samples, and fish species in April and October scrapes, represent real differences in the catch effectiveness of these gears for species within these two taxa.

Factor 2: Day vs. Night

Day-night differences were clear. None of the combined (scrape-trawl) daytime collections contained significantly more species or individuals than night collections. But nocturnal samples contained significantly more individuals than daytime samples in 69%, and more species in 62%, of the 16 day-night comparisons (Table 2).

Interactions

Significance of an interaction term indicates dependence of one factor upon the other; in this case, when sampling differences between scrape and trawl exist but are dependent upon time of day. Scrape-trawl vs. day-night interactions were significant in 8 of the 32 ANOVAs in Table 2. For these eight cases, either the trawl sampled better only at night for a certain taxon/month combination (one of the eight interactions), or the scrape sampled better only during the day (five of the eight cases), or both of these events occurred (two of the eight cases, scrape was better during the day but the trawl was better at night).

Although fish were taken in greater abundances by the trawl on three of the four sampling dates, interactions were significant on two of those dates (April and October, Table 2). With the exception of July collections, fish were equally as abundant in daytime scrape samples as in trawls (see Figure 1).

TABLE 2.—Two-way ANOVA, *F*-values. Underlined values indicate trawl samples significantly larger, all other significant values are scrape samples. All significant day-night values indicate night significantly larger than day samples.

		Decapods		Molluscs		Echinoderms		Fishes	
Date	Sample	No. indiv.	No. species	No. indiv.	No. species	No. indiv.	No. species	No. indiv.	No. species
Jan.	Day Night	0.48	35.81***	0.02	0.31	0.73	1.22	57.98***	42.14***
1979	Scrape Trawl	0.02	27.77***	56.71***	58.48***	1.92	4.29	0.44	0.08
	Interaction	0.00	5.07*	0.01	0.15	1.73	0.03	0.35	0.33
Apr.	Day Night	37.72***	31.16***	63.17***	21.41***	0.00	1.01	103.02***	29.93***
1979	Scrape Trawl	106.26***	68.13***	206.89***	55.30***	111.27***	29.71***	61.55***	27.47***
	Interaction	5.24*	0.62	22.51***	2.21	0.51	0.50	68.10***	0.03
July	Day Night	97.55*	139.64***	16.93***	24.75***	6.64*	2.79	14.06**	4.00
1979	Scrape Trawl	4.16	66.94***	70.39***	30.56***	3.06	1.72	6.93*	0.35
	Interaction	55.35***	3.67	4.32	0.29	2.57	2.48	0.03	0.09
Oct.	Day Night	7.29*	45.12***	8.03*	20.32***	1.87	3.27	20.36***	5.04*
1979	Scrape Trawl	0.42	32.14***	34.46***	99.21***	10.12**	7.91*	5.04*	9.62**
	Interaction	10.63**	0.02	5.01*	1.43	8.28**	3.20	23.85***	0.13

* = $P \leq 0.05$.
** = $P \leq 0.01$.
*** = $P \leq 0.001$.

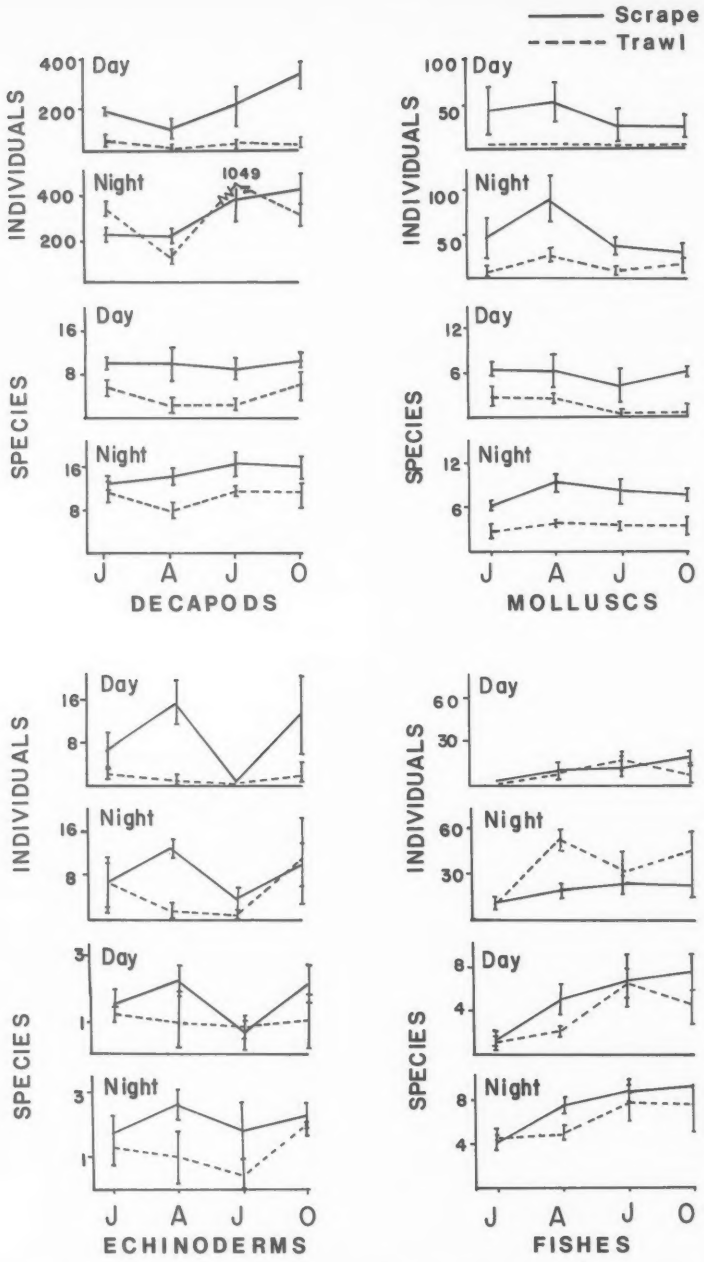

FIGURE 1.—Mean numbers of individuals and species (±1 SD) collected by the crab scrape (solid line) and trawl (dashed line) during day and night sampling in January, April, July, and October 1979.

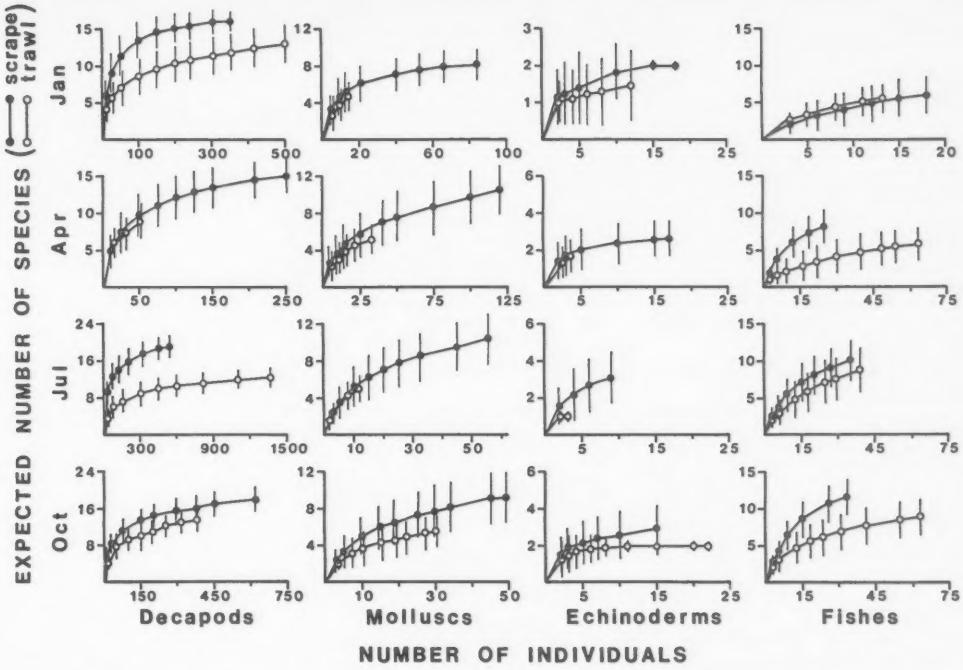

FIGURE 2.—Rarefaction curves for crab scrape (closed circles) and trawl data (open circles) from 1979 night samples. Expected numbers of species (±2 SD) are plotted against numbers of individuals. Length of curves indicates maximum number of individuals taken in any single tow.

Hence, with only one exception (July fish abundance), the otter trawl never outperformed the scrape during daylight collections.

The trawl was more effective in sampling a taxonomic group other than fish in only one case. Significantly more decapod individuals were taken in July trawl samples at night, reflecting high densities of two caridean shrimps, *Tozeuma carolinense* and *Periclimenes longicaudatus*, which appear to be more susceptable to night trawl, rather than scrape, sampling. However, decapod abundances were notably higher in July daytime collections made with the crab scrape (see Figure 1), thus the highly significant interaction term for the July analysis (decapod individuals, Table 2).

Relative Abundance

Numerical rankings of the most abundant organisms in each taxonomic group (combined over all sample dates) taken in night scrape samples are compared with those from night trawl samples in Table 3. Clear discrepancies exist between scrape and trawl estimates of species ranks and relative abundances. Relative to scrape samples, trawl collections overestimated the degree of dominance (DI = combined proportions of the two most abundant species, $(n_1 + n_2)/N$, McNaughton 1967) contributed by the most abundant shrimp *Tozeuma carolinense* and demersal fish *Gobiosoma robustum*, and underestimated dominance of the most important crab *Pagurus maclaughlinae* and mollusc *Argopectin irradians* in our samples (Table 3). Relative to trawl collections, the scrape underestimated dominance for the most abundant water-column fishes, *Lagodon rhomboides* and *Bairdiella chrysura*. Species ranks of subdominants in trawl samples also differed from rankings based on data from scrape samples.

DISCUSSION

Scrape-trawl and day-night differences in sampling effectiveness were conspicuous and generally constant throughout the year. Although more (by a fac-

TABLE 3.—Species ranks, relative abundances, and dominance for each taxonomic group. Combined night samples. $\bar{x}$ = mean number of individuals per sample (per group), DI = dominance (McNaughton 1967).

Scrape			Trawl		Scrape			Trawl	
Rank	Relative abundance		Rank	Relative abundance	Rank	Relative abundance		Rank	Relative abundance
		Shrimp					Molluscs		
1	0.324	*Tozeuma carolinense*	1	0.667	1	0.413	*Argopectin irradiens*	1	0.383
2	0.157	*Penaeus duorarum*	4	0.027	2	0.145	*Modulus modulus*	4	0.118
3	0.143	*Periclimenes longicaudatus*	2	0.191	3	0.130	*Cerithium muscarum*	6	0.077
4	0.127	*Hippolyte zostericola*	3	0.066	4	0.096	*Anachis avara*	2	0.169
5	0.099	*Thor dobkini*	6	0.016	5	0.086	*Columbella rusticoides*	3	0.131
6	0.049	*Latreutes fucorum*	5	0.018	6	0.064	*Turbo castanea*	5	0.101
7	0.049	*Ambidexter symmetricus*	8	0.003	7	0.025	*Urosalpinx perrugata*	7	0.009
8	0.038	*Alpheus normanni*	10	0.0002	8	0.013	*Nassarius vibex*	8	0.006
9	0.009	*Palaemon floridanus*	7	0.010	9	0.008	*Hyalina veliei*	—	0
10	0.006	*Periclimenes americanus*	9	0.001	10	0.007	*Fasciolaria hunteri*	—	0
$\bar{x}$ = 219.98			$\bar{x}$ = 423.38		$\bar{x}$ = 48.92			$\bar{x}$ = 13.32	
DI = 0.481			DI = 0.858		DI = 0.558			DI = 0.501	
		Crabs					Demersal Fishes		
1	0.735	*Pagurus maclaughlinae*	1	0.578	1	0.360	*Gobiosoma robustum*	1	0.544
2	0.117	*Neopanope packardii*	3	0.101	2	0.291	*Opsanus beta*	4	0.097
3	0.039	*Epialtus dilatatus*	4	0.055	3	0.246	*Paraclinus fasciatus*	2	0.194
4	0.032	*Libinia dubia*	5	0.048	4	0.086	*Centropristis melana*	3	0.106
5	0.027	*Podochela riisei*	6	0.041	5	0.017	*Ophidion beani*	5	0.058
6	0.026	*Metaporaphis calcerata*	2	0.133	$\bar{x}$ = 7.2			$\bar{x}$ = 2.6	
7	0.016	*Neopanope texana*	9.5	0.007	DI = 0.651			DI = 0.738	
8	0.004	*Pitho anisodon*	9.5	0.007					
9	0.003	*Pilumnus sayi*	7	0.018			Water-Column Fishes		
10	0.002	*Pilumnus dasypodus*	8	0.011	1	0.345	*Lagodon rhomboides*	1	0.621
$\bar{x}$ = 75.1			$\bar{x}$ = 10.9		2	0.158	*Monacanthus ciliatus*	4	0.044
DI = 0.852			DI = 0.711		3	0.154	*Syngnathus floridae*	5	0.042
					4	0.151	*Orthopristis chrysoptera*	3	0.099
		Echinoderms			5	0.067	*Hippocampus zosterae*	7	0.007
1	0.659	*Echinaster* sp.	1	0.824	6.5	0.052	*Microgmathus crinigerus*	8.5	0.002
2	0.255	*Ophiothrix angulata*	2	0.176	6.5	0.052	*Haemulon plumieri*	6	0.013
3	0.056	*Lytechinus variegatus*	—	0	8	0.015	*Bairdiella chrysura*	2	0.168
4	0.027	*Ophioderma brevispinum*	—	0	9	0.004	*Monacanthus hispidus*	8.5	0.002
$\bar{x}$ = 8.42			$\bar{x}$ = 5.12		$\bar{x}$ = 11.5			$\bar{x}$ = 31.7	
DI = 0.914			DI = 1.00		DI = 0.503			DI = 0.789	

tor of 4.6) substratum surface area was sampled per tow by the otter trawl, the crab scrape collected more species and individuals per tow, across taxa, with few exceptions. The trawl was the better faunal collecting gear in this seagrass habitat only for numbers of individuals of certain water-column fishes and for two species of caridean shrimps. The scrape was notably more effective than the trawl (day and night) for collecting penaeid, alpheid, and processid shrimps, brachyuran and pagurid crabs, molluscs, echinoderms, syngnathid fishes, and demersal fishes (*Opsanus*, *Paraclinus*, *Gobiosoma*, and *Centropristis*).

The otter trawl appears to collect fewer species and individuals of demersal animals in grassbeds than does the scrape because the weighted (tickler) chain on the trawl is not in contact with the substratum. Under tow, the cylindrical bottom crossbar of a crab scrape bends grassblades flat against the substratum, sweeping demersal and epifaunal organisms over the bar and into the net, whereas the otter trawl tickler chain is generally supported 8-10 cm above the substratum by the buoyant vegetation (Leber, pers. obs.). Grassblades do not yield as much to the relatively light weight of a tickler chain (as they do to a scrape crossbar), and any organisms remaining close to the substratum as the chain passes over them evade capture. Most epibenthic inhabitants of grassbeds, including several fishes, are more closely associated with seagrasses and red drift algae than with the water column above the vegetation or bare patches within beds (Hooks et al. 1976; Heck and Wetstone 1977; Stoner 1980; Stoner and Livingston 1980; Gore et al. 1981). The crab scrape is more effective because it samples more grassblade surface area, including an additional microhabitat, the region <10 cm above the substratum (Leber, pers. obs.).

The greater effectiveness of both devices at night is probably accounted for, in part, by nocturnal increases in faunal activity on the substratum, on blade tips, and in the water column above vegetation.

Several crustaceans emerge from the substratum and forage at night in grassbeds, including pink shrimp, *Penaeus duorarum*, some majid crabs (notably *Pitho* and adult *Libinia* at our site), and alpheid and processid shrimps (Fuss 1964; Fuss and Ogren 1966; Hughes 1968; Kikuchi and Peres 1977; Saloman 1979; Greening and Livingston 1982; Leber 1983). Emergence of nocturnal organisms from the substratum after dark would explain some of the variability between day and night collections of invertebrates. Higher densities of diurnally active animals in night samples may be due to nocturnal vertical migrations up grass-blades. Animals located near the tips of blades are clearly more vulnerable to capture by either device; even the scrape misses individuals trapped between grass-blades and substratum by the crossbar, an event less likely to occur to an individual near a blade tip. Fishes were probably less abundant in daytime trawl collections because of avoidance reactions to the clearly visible net.

Emergence and vertical migration do not account for all of the increases in invertebrate abundance in night samples. The case of the arrow shrimp, *Tozeuma carolinense*, is interesting in this regard. We expected no day-night sampling differences for *Tozeuma* with either device, based on evidence that *Tozeuma* inhabit the region near tips of grass-blades, both during the day and at night (Main in press). As expected, *Tozeuma* were collected in roughly equal numbers in both day and night scrape samples. However, almost an order of magnitude more *Tozeuma* were taken in night trawl samples than during daytime collections (Leber and Greening, unpubl. data). It appears that *Tozeuma* may be capable of avoiding the trawl, which is highly visible during the day. These shrimp have keen vision in daylight and are capable of rapid movement (up to 30 cm) via a caridoid escape response (Main in press). They need only move down blades, closer to the substratum, to avoid the trawl net.

This study suggests that many demersal fishes and epibenthic invertebrates may be more important numerically in seagrass communities than indicated by collections made with an otter trawl. Species ranks and relative abundances of these organisms determined from trawl collections in seagrass beds should be interpreted with care. Whereas trawl collections may be satisfactory for monthly or year-to-year comparisons of single species abundances within a seagrass habitat, application of such data to examination of predatory-prey relationships (e.g., energy flow and optimal-diet models) or other biotic interactions in grassbeds may lead to erroneous interpretations. The combined approach of day-night sampling with both an otter trawl (for water-column fishes) and a crab scrape (for demersal organisms) is recommended for seagrass studies.

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NOTES

A PRELIMINARY INVESTIGATION OF THE STOCK STRUCTURE OF THE DOLPHIN, *CORYPHAENA HIPPURUS*, IN THE WESTERN CENTRAL ATLANTIC

Dolphin, *Coryphaena hippurus*, are fast swimming, migratory, pelagic fish, which support commercial and sport fisheries throughout the western central Atlantic (Erdman 1956; Zaneveld 1961; Beardsley 1967; Rose and Hassler 1969; Sacchi et al. 1981; Olsen and Wood 1982). In terms of weight and revenue, they are the most important large pelagic fish landed by the commercial fisheries in the southeastern Caribbean (Mahon et al. 1981). In the northwest, they are the most important sport fish, being taken on more trips and in greater numbers by charter boats in Florida (Ellis 1957; Iversen 1962) and in North Carolina (Hassler and Hogarth 1977; Rose and Hassler 1969) than any other species. Rapid expansion of the dolphin fishery fleets is currently underway in the eastern Caribbean, but the biological data necessary for management have not been gathered. For example, we remain ignorant of the number and distribution of stocks of *C. hippurus* in the western central Atlantic.

Regional dolphin fisheries are markedly seasonal and this presumably results from migration; but migration patterns remain largely unknown (Palko et al. 1982). However, Beardsley (1967) believed that dolphin migrate northwards during spring and summer, and Gibbs and Collette (1959) suggested that the spring abundance of *C. hippurus* in the Caribbean may be a prespawning migration, mostly by females. A preliminary survey of regional catch records indicates a staggering of the peak fishing seasons, which supports the assumption that migration is large-scale (Hunte and Mahon 1982).

In the present paper, we take three approaches to our investigation of *C. hippurus* in the western central Atlantic: 1) We use commercial and sport fishing data from several countries to examine seasonality and size structure of catch throughout the region; 2) we compare growth, age/size at sexual maturity, fecundity, and egg size of dolphin from different parts of the region; 3) we use electrophoretic techniques to compare dolphin sampled from Miami and Barbados, two widely spaced fisheries in the region. Electrophoretic techniques, combined with histochemical staining for isozymes, are now widely recognized as a useful tool for examining genetic affinities between fish stocks (Iwata 1975; Allendorf 1979; McGlade 1981; Ihssen et al. 1981; Ferris et al. 1982). By these means, we address the question of whether the dolphin fisheries in the western central Atlantic exploit a single stock migrating through the region or distinct units located in geographically contiguous areas. Resolution of this question will affect the extent to which individual territories should expand their dolphin fisheries, will determine whether management programs need be regional or territory-specific, and will identify which territories need to collaborate for joint management of stocks.

Methods

Dolphin monthly catch data, recorded by commercial or sport fisheries, were obtained either by letter, personal visit to fisheries departments, and/or published literature (Table 1). The catch data, recorded as numbers, weights, catch per day or per boat, and over time periods of 1 to 12 years, were standardized and plotted as percentages of total annual catch landed each month. Where more than 1 year's data were available, the average catch each month was calculated.

Tissue samples for the electrophoretic survey were collected off Barbados between December 1982 and March 1983, and off Miami in May and June 1983. Samples of eye, heart, liver, gonad, and white muscle were taken from a total of 1,669 freshly landed dolphin and were deep frozen for later analysis. A survey of 22 enzymes encoded by 55 presumptive loci was conducted to identify polymorphic enzyme systems. The allelic frequencies of the highly polymorphic isocitrate dehydrogenase, Idh-2, locus were compared in Miami and Barbados dolphin. The horizontal starch gel electrophoresis methodology follows that of May et al. (1979) and McGlade et al. (1983). Allelic nomenclature follows that of Allendorf and Utter (1979).

Life history data were obtained from the literature, from records of length and weight of specimens caught in the Bahamas, Bermuda, and North Carolina, and from our own studies of 624 dolphin landed during the peak of the sport fishery in Miami and 3,126 dolphin landed by the commercial fishery in Barbados.

TABLE 1.—Countries from which catch data on the dolphin, *Coryphaena hippurus*, were obtained, with the data source for each country.

Territory	Data source	Time period
Curacao	Zaneveld (1961)	1957-58
Grenada	J. Finlay, Fisheries Officer, Ministry of Agriculture, National Resources and Industrial Development, St. George's, Grenada.	1981-83
St. Vincent	K. Morris, Fisheries Officer, Ministry of Agriculture and Fisheries, Kingstown, St. Vincent.	1975-81
Barbados	R. Hastings and P. McConney, Fisheries Officers, Fisheries Division, Bay Street, Bridgetown, Barbados.	1973-82
St. Lucia	P. Murray, Fisheries Biologist, Ministry of Agriculture, Lands, Fisheries, and Cooperatives, Fisheries Division, Castries, St. Lucia.	1978, 1980-82
Martinique and Guadeloupe	Sacchi et al. (1981)	1980
Virgin Isles	R. Wood, Fisheries Biologist, Department of Conservation and Cultural Affairs, Division of Fish and Wildlife, St. Thomas, Virgin Islands.	1967-78
	Olsen and Wood (1982)	
Puerto Rico	Erdman (1956)	1951-56
	O. Munoz-Roure, Executive Director, Caribbean Fisheries Management Council, Hato Rey, Puerto Rico.	
Bahamas	P. Major, Fisheries Biologist, Ministry of Agriculture, Fisheries, and Local Government, Nassau, Bahamas.	1976, 1978
Florida	A. Jones, Fisheries Scientist, Southeast Fisheries Center, NMFS, NOAA, Miami, Florida.	1970-80
	Fable et al. (1981)	1971-79
Georgia	A. Jones, see Florida	1978-79
South Carolina	A. Jones, see Florida	1976-80
North Carolina	A. Jones, see Florida	1978-80
	Manooch and Laws (1979)	1977
	Rose and Hassler (1969)	1961
Bermuda	B. Luckhurst, Fisheries Officer, Ministry of Fisheries and Agriculture, Naval Base, Southampton, Bermuda.	1973-80

RESULTS AND DISCUSSION

Seasonality and Size Structure of Catch

The seasonality of dolphin catch in 14 territories is shown in Figure 1. Martinique and Guadaloupe supplied no data, but information was given on the duration and peak of the dolphin season. It should be noted that the U.S. Virgin Islands is the only territory with a distinctly bimodal catch pattern.

The peak months of catch in each territory are superimposed on a map of the western central Atlantic in Figure 2. Grenada peak catch is in February/March; Barbados, St. Vincent, and St. Lucia in March/April; Martinique and Guadeloupe in April; and the Virgin Islands in April/May, giving the Virgin Islands their first and largest annual peak. This pattern of catch seasonality is suggestive of a stock (subsequently called the southern stock) moving northwest through the island arc. If the stock then turned west and moved past Puerto Rico, we would expect peak catch there to be between June, July, and August; but this is when Puerto Rico catches the least dolphin (see Figure 1). We therefore suggest that, on leaving the Virgin Islands, the stock moves northeasterly into the Atlantic, completing a circuit and returning to Grenada by February/March of the following year. This implies that there is a second stock (subsequently called the northern stock) located in the northwest region of the western central Atlantic. It occurs near Puerto Rico between December and February. It next moves northwesterly past the Bahamas in April/May, Florida and Georgia in May/June, South and North Carolina in June/July, and Bermuda in July/August. It then completes its circuit by passing through the Virgin Islands, giving that territory its second and smaller peak in November and returning to Puerto Rico by December/February.

The mean size of fish caught in five territories during peak fishing season is shown in Figure 3, and the size structure of the catch throughout the fishing season in Barbados is shown in Figure 4. The data are consistent with the migration circuits proposed. In the northern stock, small presumably young-of-the-year fish are predominant during the summer when the stock is near Florida, North Carolina, and Bermuda. The mean size taken by the sport fishery in Florida is 1.69 kg; in North Carolina, where they occur 1 mo later, it is 2.92 kg; and in Bermuda, where they occur 2 mo later, it is 3.85 kg. These differences presumably reflect growth within the cohort. The largest fish are taken by Puerto Rico, where Erdman (1956) reported that dolphin up to 23 kg in weight occur during the peak winter fishing season, and by the Bahamas where the mean weight during the peak fishing months is 6.45 kg. This suggests

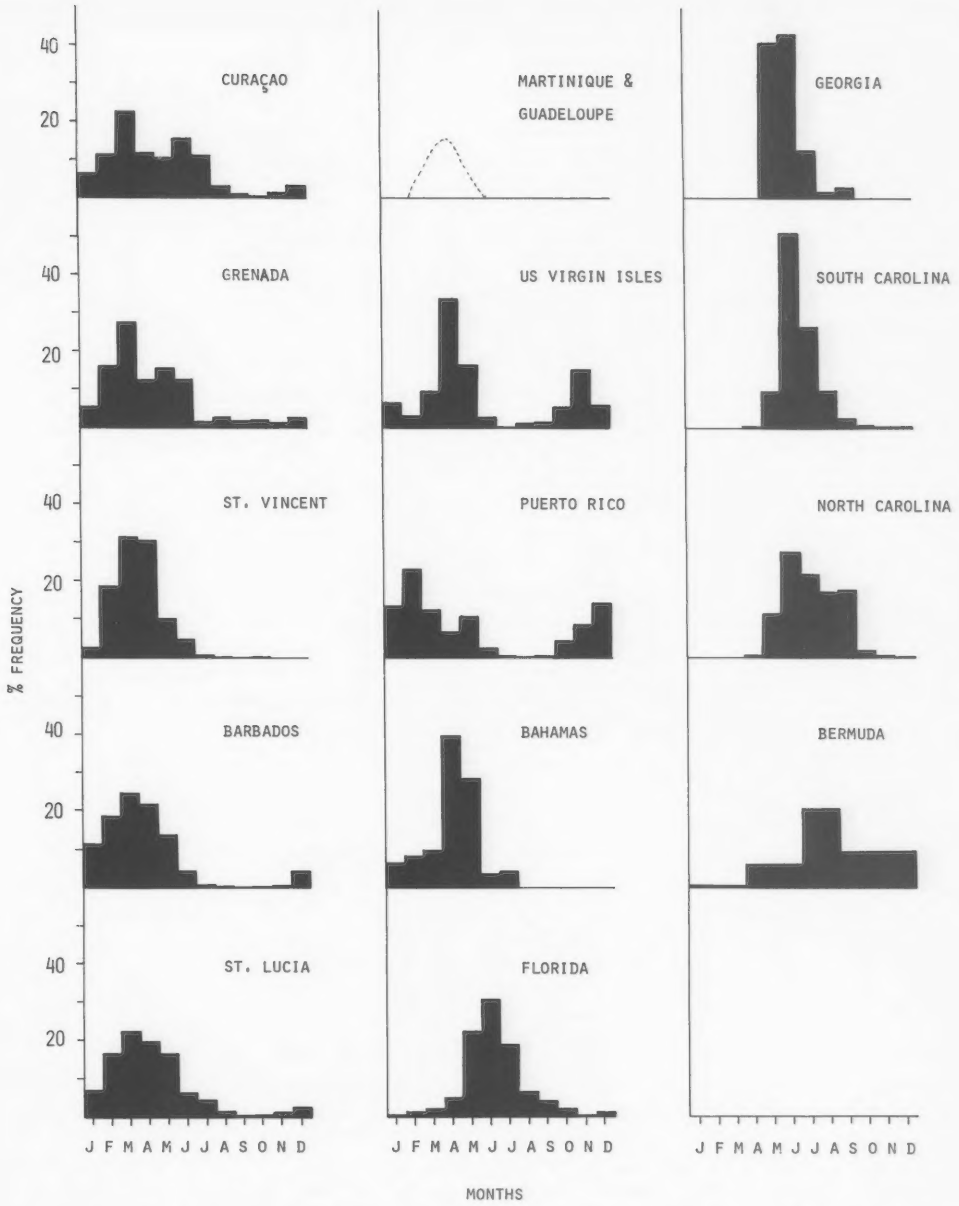


FIGURE 1.—Seasonality of the dolphin, *Coryphaena hippurus* fisheries in the western central Atlantic, shown in geographical order from south to north. Note that raw catch data were not available from Martinique and Guadeloupe, but the duration of season and peak month were known.

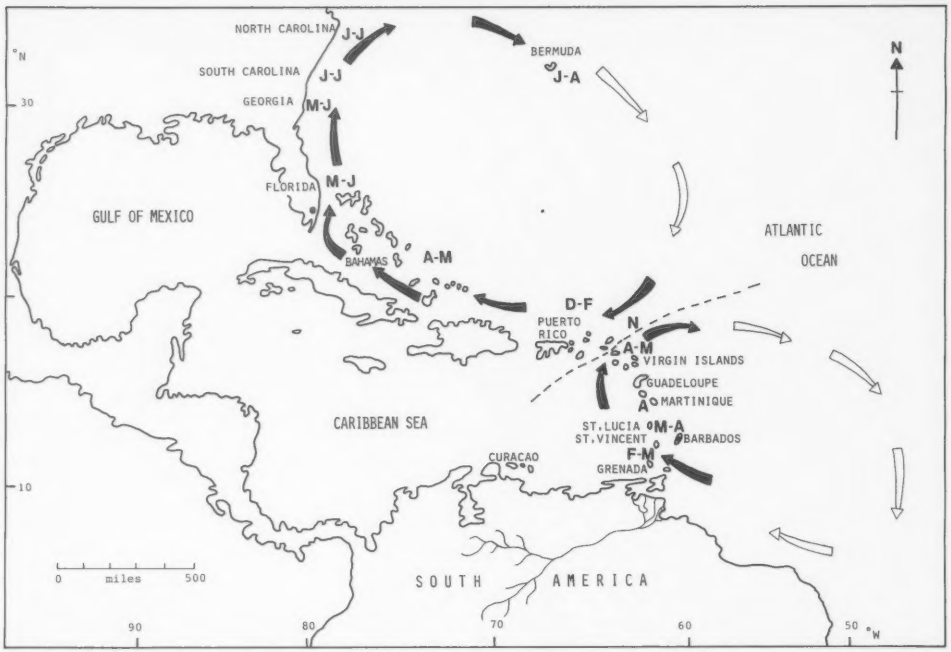


FIGURE 2.—Months of peak catch of the dolphin, *Coryphaena hippurus*, and proposed migration circuits for northern and southern dolphin stocks in the western central Atlantic. Letter symbols (e.g., A-M) indicate months of peak catch. ➡ indicate proposed migration. ⇨ indicate proposed migration where catch data were not available. • indicate locations from which samples for electrophoresis were collected.

continued growth of the cohort as it leaves Bermuda and returns southwards into the northern Caribbean for the winter. Note that since dolphin are serial spawners and since fecundity is proportional to size (Beardsley 1967; Oxenford and Hunte in press), most spawning by a cohort will occur when the dolphin comprising it are large. For the northern dolphin, this would be when the stock is near Puerto Rico, i.e., at the southeastern or up-current limit of their range. Peak spawning near Puerto Rico is reported to occur in early spring (Erdman 1976) and presumably produces the small young-of-the-year fish caught near Florida during the summer.

The size structure of dolphin caught at Barbados (Fig. 4) is consistent with the proposed migration for the southern stock. In February, the main cohort is composed of fish about 5½ mo old with a mean standard length of 812.24 mm. Growth within this cohort occurs throughout the fishing season to June, when the average fish size is 1,007.83 mm SL (Oxenford and Hunte 1983). After this, abundance drops sharply (Fig. 1) as the cohort leaves Barbados

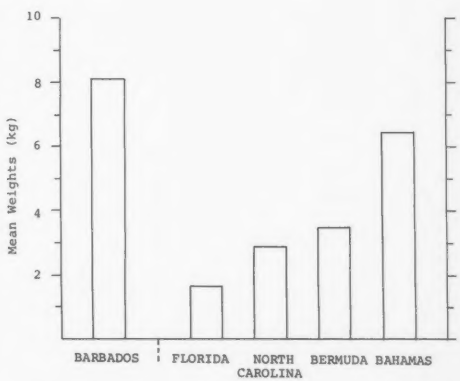


FIGURE 3.—Mean weights of individuals of the dolphin, *Coryphaena hippurus*, landed during peak fishing seasons at five locations in the western central Atlantic.

migrating northwards. During early summer (June/July) and early autumn (October), the presence of

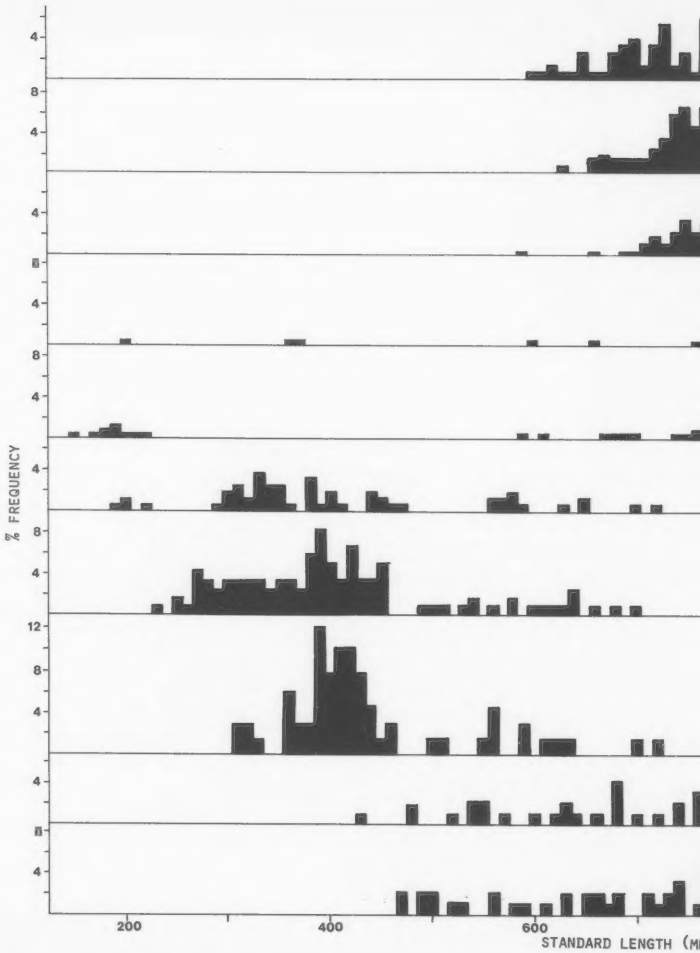
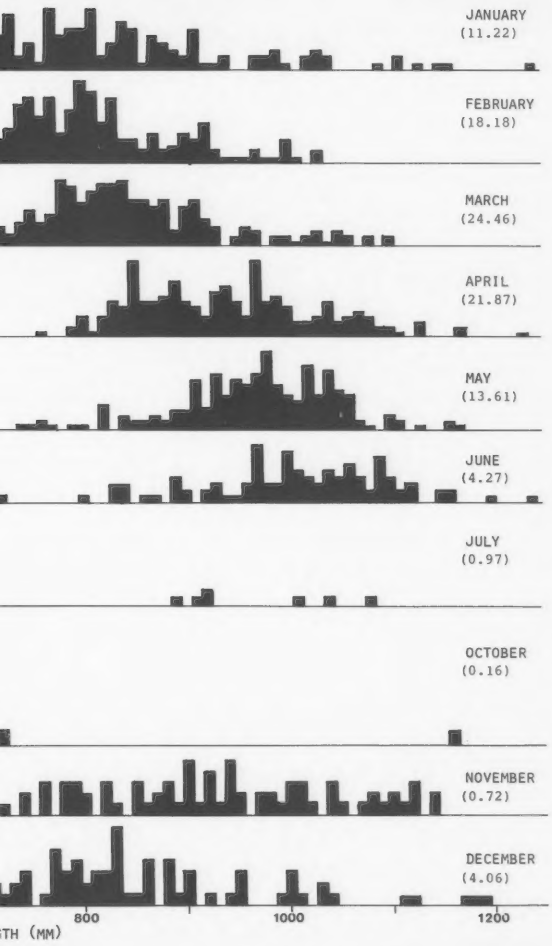


FIGURE 4.—The size-structure of the dolphin, *Coryphaena hippurus*, landed by the Barbados comme
of total annual catch by weight landed e



commercial fishery over 10 mo. The values in parentheses are the percentage
nded each month.

a few very small dolphin (<2% of the annual catch by weight), landed as bycatch of the flying fish fishery (see Figure 4), indicates the arrival of the first of the young-of-the-year group, with a few very large mature adults from the previous year. Note that many of these young-of-the-year are already mature on reaching Barbados in November, and all are ripe by the time the cohort leaves Barbados in June. Note too, that aging of the cohort (Oxenford and Hunte 1983) suggests that the cohort was spawned between September and January, when the parent stock would be towards the southeastern, up-current extreme of the proposed migration circuit.

Life History Comparisons

Data on life history parameters of dolphin from northern and southern circuits are summarized in

TABLE 2.—Life history characteristics of the dolphin *Coryphaena hippurus* in the western central Atlantic.

Life history characteristics		Location	Data Source
Northern area:			
Average 1st year growth rate (mm SL/d)	≈ 1.64 ≈ 1.82	N. Carolina Florida	Rose and Hassler (1968) Beardsley (1967)
Length-weight relationship in the form $y = ax^b$ (y is weight (kg) x is SL (mm))	Males: $y = 0.05 \times 10^{-8}\ x^{2.75}$ $y \approx 1.45 \times 10^{-7}\ x^{2.58}$ Females: $y = 1.27 \times 10^{-7}\ x^{2.59}$ $y \approx 5.75 \times 10^{-8}\ x^{2.71}$	N. Carolina Florida N. Carolina Florida	Rose and Hassler (1968) Beardsley (1967, fig. 7) Rose and Hassler (1968) Beardsley (1967, fig. 7)
Fecundity-length relationship in the form $y = ax^b$ (y is mature egg numbers x is FL (mm))	$y \approx 2.52 \times 10^{-4}\ x^{3.12}$	Florida	Beardsley (1967, fig. 11)
Size at first maturity (mm SL)	Males: 393 Females 324	Florida	Beardsley (1967)
Age at first maturity (months)	≈ 6-7	Florida	Beardsley (1967)
Mature egg size range (mm diameter)	1-1.7	Florida	Beardsley (1967, fig. 9)
Mean mature egg size (mm diameter)	1.3	N. Carolina	Hassler and Rainville (1975)
Spawning season	Extended	Atlantic	Shcherbachev (1973) Fahay (1975) Johnson (1978)
		Florida Current	Gibbs and Collette (1959) Beardsley (1967)
Age structure (% which are <2 yr)	96 98	N. Carolina Florida	Rose and Hassler (1968) Beardsley (1967)
Southern area:			
Average 1st year growth rate (mm SL/d)	≈ 4.17	Barbados	Oxenford and Hunte (1983)
Length-weight relationship in the form $y = ax^b$ (y is weight (kg) x is SL (mm))	Males: $y = 1.24 \times 10^{-8}\ x^{2.94}$ Females: $y\ 2.22 \times 10^{-8}\ x^{2.84}$	Barbados	Oxenford and Hunte (in press)
Fecundity-length relationship in the form $y = ax^b$ (y is mature egg numbers x is FL (mm))	$y = 2.7 \times 10^{-6}\ x^{3.67}$	Barbados	this study
Size at first maturity (mm SL)	Males: 735 Females: 610	Barbados	this study
Age at first maturity (months)	≈ 4	Barbados	this study
Mature egg size range (mm diameter)	0.86-1.00	Barbados	this study
Mean mature egg size (mm diameter)	0.97	Barbados	this study
Spawning season	Extended	Barbados	this study
Age structure (% which are <2 yr)	100	Barbados	Oxenford and Hunte (1983)

Table 2 and are not supportive of a single stock hypothesis. Dolphin in Barbados waters appear to grow faster (Oxenford and Hunte 1983) than those in North Carolina (Rose and Hassler 1968) and Florida (Beardsley 1967). Note that scale annuli are found in northern dolphin but not in southern dolphin; a difference supportive of the assertion that the two groups are distinct. Beardsley (1967) suggested that the formation of the dolphin scale annuli at Florida was correlated with the temperature reduction occurring in the Florida Current during winter.

Dolphin from Barbados are larger but younger at first sexual maturity than those from Florida. Fecundity increases with fish size in both groups, but Florida dolphin have higher fecundity at size than Barbados dolphin (Oxenford and Hunte in press). Mature eggs taken from Florida and North Carolina dolphin are apparently larger than those from Barbados dolphin. Intraspecific variation in egg size is seldom environmental and is typically a function of fish age (Bagenal 1971; Kazakov 1981). Mature egg size does not increase with fish size/age for Barbados dolphin (linear regression, $r = 0.353$ $b = 0.0001$). Therefore, assuming that the differences observed in egg size of southern and northern dolphin do not result merely from differences in investigators' methodologies, they are suggestive of separate stocks as shown for different spawning groups of herring (Blaxter and Hempel 1963; Cushing 1967) and sockeye salmon (Foerster 1968; Bagenal 1971).

Electrophoretic Comparisons

In the electrophoretic survey, 55 presumptive loci could be consistently scored. Of these, 39 were fixed for the same alleles in both samples, and a further 12 were close to fixation. Two isocitrate dehydrogenase loci (Idh-2,3) and two esterase loci (Est-1,2) had alternate alleles at a frequency >0.05, i.e. were significantly polymorphic.

Seven phenotypes were observed at the Idh-2 locus expressed in heart tissue (Fig. 5). The pattern of activity at this locus is typical of an active dimeric enzyme with disomic inheritance (Darnall and Klotz 1972; Kirpichnikov 1981) and four alleles with relative mobilities to 100, 123, 86, and 68. Thus, putative genotypes could be assigned to the observed phenotypes as indicated in Figure 5, and allelic frequencies calculated (Table 3). Unequivocal assignation of genotypes to the phenotypes, observed at the remaining polymorphic loci, was not possible in the absence of inheritance data, since the loci have alleles with overlapping mobilities. Idh-3 and Idh-2, expressed together in liver tissue, both have alleles with relative mobilities to 100, 123, and 86, and although the asymmetrically banded phenotypes could be easily read, the presence of a null allele at Idh-3 meant that certain phenotypes could have been produced by a number of different genotypes. Est-1 and Est-2 share all or some of four alleles, but the banding intensity ratios of individual phenotypes could not be determined. Hence, assignation of genotypes to phenotypes at these loci was not possible. In summary, only the Idh-2 locus, expressed independently from Idh-3 in heart tissue, was considered suitable for a comparison of Miami and Barbados dolphin.

The frequencies of alleles at Idh-2 differed significantly in the two populations (chi-square 2 × 4 contingency test: $\chi^2 = 12.725$, df = $(r - 1)(C - 1) = 3$, $0.01 > P > 0.0005$; Table 3). Note that the varia-

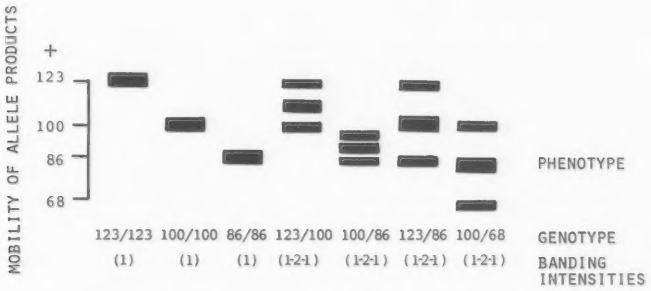


FIGURE 5.—A starch-gel zymogram of the dimeric enzyme isocitric dehydrogenase, showing the phenotypes observed and putative genotypes at the Idh-2 locus in heart extracts of the dolphin, *Coryphaena hippurus*, from the western central Atlantic. Values in parentheses are ratios of allele products.

TABLE 3.—Observed allelic frequencies (obs. freq.) and number (obs. no.) of alleles at the Idh-2 locus in heart tissue of the dolphin, *Coryphaena hippurus*, from Miami and Barbados. Expected values (exp. no.) refer to the number expected if the samples do not differ.

Sample location	No. of fish		Alleles			
			68	86	100	123
Miami	539	obs. freq.	0.0009	0.3154	0.6660	0.0176
		obs. no.	1	340	718	19
		exp. no.	(0.47)	(304.14)	(751.56)	(21.83)
Barbados	597	obs. freq.	0.0000	0.2521	0.7253	0.0226
		obs. no.	0	301	866	27
		exp. no.	(0.53)	(336.86)	(832.44)	(24.17)

tion observed at Idh-2 did not differ from that predicted under Hardy-Weinberg equilibrium for either population (chi-square goodness of fit: for Barbados, $\chi^2 = 6.337$, df = 3, $0.25 > P > 0.1$; for Miami, $\chi^2 = 9.9145$, df = 6, $0.25 > P > 0.1$; Table 4).

The differences in life history traits of Miami and Barbados dolphin could in principle be environmental. The genetic differences observed at the Idh-2 locus suggest that there may be little gene flow between the northern and southern groups; but could in theory result from a regional cline. The primary evidence supporting our suggestion of more than one dolphin stock in the western central Atlantic is therefore the seasonality of catch data and the mean size of dolphin landed in each territory. Taken together, the three data sets certainly suggest that the assumption of a single stock may be unjustified. Efforts should now be made to test the two stock hypothesis proposed and to investigate the possible presence of additional dolphin stocks, particularly in the western Caribbean Sea and in the Gulf of Mexico.

TABLE 4.—The number of each phenotype observed (obs.) at the Idh-2 locus in heart tissue of the dolphin, *Coryphaena hippurus*, from Barbados and Miami. Expected values (exp.) refer to the numbers expected if the populations are in Hardy-Weinberg equilibrium.

Putative genotype for Idh-2		Sample location	
		Barbados (n = 597)	Miami (n = 539)
86/86	obs.	47	64
	exp.	(37.94)	(53.62)
100/86	obs.	199	205
	exp.	(218.31)	(226.46)
100/100	obs.	325	251
	exp.	(314.05)	(239.11)
100/123	obs.	17	10
	exp.	(19.58)	(12.65)
123/123	obs.	1	1
	exp.	(0.31)	(0.17)
123/86	obs.	8	7
	exp.	(6.81)	(5.99)
68/68	obs.	—	0
	exp.		(0.00)
100/68	obs.	—	1
	exp.		(0.67)
123/68	obs.	—	0
	exp.		(0.02)
86/68	obs.	—	0
	exp.		(0.32)

Acknowledgments

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EFFECTS OF TEMPERATURE ON SWIMMING SPEED OF THE DINOFLAGELLATE *GYMNODINIUM SPLENDENS*

Dinoflagellate blooms or red tides frequently occur in a stratified water column having low nutrients near the surface (Huntsman et al. 1981). Under these conditions dinoflagellates have a competitive advantage over other phytoplankton due to their motility and diel vertical migration pattern. In the absence of turbulence, active swimming allows them to overcome sinking and thereby, remain close to the surface. The normal diel vertical migration consists of an ascent to some minimum depth during the day and descent to a maximum depth at the night (reviewed by Forward 1976). Through this pattern they have access to nutrients over the area covered by migration and they can migrate to the surface during the day to obtain more light for photosynthesis (Ryther 1955; Margalef 1978; Huntsman et al. 1981).

The success of dinoflagellates depends to a great extent upon their swimming capability. There have been few measurements of actual swimming speeds of individual dinoflagellates (e.g., Hand et al. 1965) or estimates of speeds from population movements during migration (Eppley et al. 1968; Kamykowski and Zentara 1977). This is unfortunate because such measurements are necessary to estimate the depth of the water column available to dinoflagellates for nutrients during migration.

The most pronounced and widespread dinoflagellate blooms off the coast of Peru are caused by *Gymnodinium splendens* Lebour. Blooms occur most frequently during the summer and are usually associated with the phenomenon of El Niño (Rojas de Mendiola 1979). At the beginning of the 1976 El Niño, there was a major bloom of *G. splendens*. Blasco's (1979) surface measurements during this bloom indicated the dinoflagellate vertically migrated with the suggested pattern involving an ascent in the early morning and maintenance of a deeper distribution at night. This pattern was similar to that observed by Kiefer and Lasker (1975) for this species in the Gulf of California. Vertical chlorophyll a profiles indicated the cells rose in the morning and descended in the evening. The present study was undertaken to measure swimming speeds of *G. splendens* under different temperature conditions. The observed speeds vary with temperature and are similar to those calculated from field studies.

Materials and Methods

The dinoflagellate *Gymnodinium splendens* Lebour was cultured as described previously (Forward 1974) in a Sherer[1] environmental chamber (Model CEL-44) on a 14:10 LD cycle at a salinity of about 34 ppt. All experiments were performed in the middle 4 h of the light phase with cultures having densities of about 2,000 cells/mL. This cell density was used because it was similar to that used in past studies (Forward 1974, 1977) and thus past results can be applied to the present study. Swimming speed during phototaxis was only measured during a specific time interval because there is a circadian rhythm in phototaxis (Forward 1974). *Gymnodinium splendens* shows about average levels of phototaxis during the middle 4 h of the light phase. It is not known whether there is a similar rhythm in swimming.

Subcultures were exposed to two sets of temperature conditions to test for the effects of 1) temperature acclimation and 2) acute temperature changes upon swimming speed. In the first tests cells were acclimated to selected temperatures from 13° to 25°C for at least 5 d prior to swimming speed measurements. These temperatures were used because they encompass the range in which the cells grow at reasonable rates (Thomas et al. 1973). For the second tests, cultures were acclimated to 19°C for at least 5 d. At the time of testing cultures were exposed to an acute temperature change by placing the flasks in a water bath set at selected temperatures for 0.5 h, after which time swimming speed was measured. Room lights were on during this 0.5-h period. The temperature of the room in which swimming was measured was regulated to approximately each test temperature. Each test was performed on four separate subscultures.

To measure swimming speeds, a sample of cells was removed from a subculture and placed in a clear

[1]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

cuvette. The cells were viewed by the closed circuit video system described by Forward (1974). During random swimming the cells can move in any direction and are not necessarily moving in the plane of view of the video camera. Thus measurements of swimming speeds during random swimming tend to underestimate true speed. To prevent this problem, cells were stimulated horizontally with light and speed measured during oriented swimming toward the light (positive phototaxis). Room lights were off during light stimulation.

The light stimulus was a tungsten light source filtered with a 4-96 Corning filter. The spectral composition of the light was similar to the spectral sensitivity of phototaxis of *G. splendens* (Forward 1974). A constant light intensity of 4.79×10^2 Wm^{-2}, as measured with an EG and G radiometer (Model 550) and calculated at 465 nm, was used for all tests because maximum positive phototaxis occurs in this intensity range, and it was necessary to measure swimming speed during phototaxis. Swimming was recorded on video tape and speed analyzed using previous techniques (Forward 1974).

Results

Swimming speed varied greatly with temperature (Fig. 1) as mean speeds approximately double upon acclimation to temperatures between 13° and 25°C (0.56 h^{-1} to 1.16 mh^{-1}). The dinoflagellate seems capable of limited temperature acclimation. If the cells were acclimated to 19°C and suddenly exposed to other temperatures, there was always a significant difference (Student's t test; $P < 0.001$) between these mean speeds and those upon acclimation. At a lower temperature of 13°C the acclimation speed was higher; while at temperatures above 19°C, the acclimation speeds were lower. This trend is expected with acclimation.

The effects of temperature can be further assessed by calculating the temperature coefficients upon acclimation and exposure to acute temperature changes (Table 1). The Q_{10} values for acute changes are always higher than those upon acclimation, which is expected if swimming rates are adjusted through acclimation. When acclimated to temperatures between 13° and 19°C, the cells showed total compensation ($Q_{10} = 0.98$). In contrast, they were less able to adjust their rates upon acclimation to higher temperatures between 19° and 25°C ($Q_{10} = 3.42$). Partial acclimation occurred over this temperature

TABLE 1.—Temperature coefficient values for the dinoflagellate *Gymnodinium splendens* upon temperature acclimation and exposure to acute changes in temperature.

Temperature range	Acute Q_{10}	Acclimation Q_{10}
13°-19°C	1.47	0.98
19°-25°C	4.68	3.42

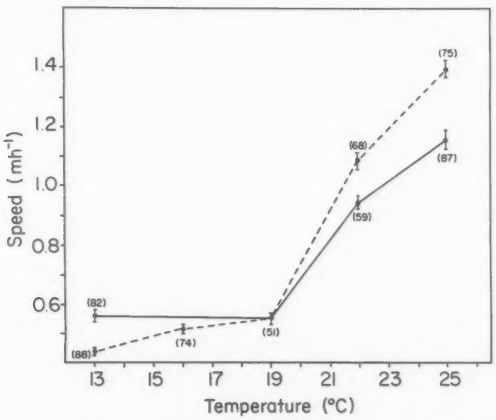

FIGURE 1.—Swimming speeds of the dinoflagellate *Gymnodinium splendens* upon acclimation to various temperatures (solid line). The effect of acute temperature change was measured by acclimating the animals to 19°C and measuring speeds upon exposure to other temperatures (dashed line). The number beside the points are the sample sizes and the vertical bars are standard errors.

range since the acclimation Q_{10} is lower than the acute Q_{10} (Table 1).

Discussion

Blooms of *G. splendens* occur off the coast of Peru in temperatures ranging from 17° to 23°C with optimum being 18°-21°C (Rojas de Mendiola 1979). The lower temperature agrees with laboratory measurements of vertical migration, as Kamykowski (1981) found migration in the laboratory occurred at temperatures above 16°C. In the laboratory, this dinoflagellate can survive and divide at temperatures from 12° to 29°C. The most rapid growth rates (0.4 divisions/d), however, occur at 20°-27°C (Thomas et al. 1973). Within the optimum temperature range suggested from these studies (18°-26°C), swimming speed of *G. splendens* approximately doubles (Fig. 1). These speeds and their change with temperature are similar to those reported for other dinoflagellate species (Hand et al. 1965).

The speeds of movement calculated from field studies of vertical migration of *G. splendens* agree with the speeds found in the present study. Blasco (1979) calculated that a speed of 1 m/h was sufficient to account for the migration off Peru during the 1976 El Niño. In the Gulf of California, *G. splendens* migrated over a depth of about 9 m and had a calculated descent velocity at sunset of 1.7 m/h (Kiefer and Lasker 1975). The present study predicted this speed would occur at temperatures above 25°C. Unfortunately Kiefer and Lasker (1975) did not state the water temperature at the time of migration.

An objective of the present study was to use the measured swimming speeds to determine the distance over which *G. splendens* should be capable of migrating. A conservative estimate of distance can be calculated from the speeds upon acclimation to optimum temperatures (19°-25°C) and assuming the dinoflagellate 1) swims continuously in either the upward or downward direction for half of the migration cycle (12 h) and 2) does not have a diel rhythm in swimming speed. At 19°, 22°, and 25°C the calculated distances are 6.6, 11.3, and 13.9 m respectively. These distances would increase slightly if a temperature gradient existed because speed is approximately constant at 19°C and lower temperatures, and acute exposure to higher temperatures, which would occur high in the water column, would elevate speeds above those upon acclimation (Fig. 1). In addition, these values would probably vary if *G. splendens* is exposed to different environmental conditions, since salinity, light intensity, and nutrient levels can affect migration patterns (Kamykowski 1981).

Acknowledgments

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MORPHOLOGY AND POSSIBLE SWIMMING MODE OF A YELLOWFIN TUNA, *THUNNUS ALBACARES*, LACKING ONE PECTORAL FIN

In September of 1982, the Mexican bait boat, *Paesa*, fishing off Baja California, captured a 36.5 cm fork length (861.2 g wet weight) yellowfin tuna, *Thunnus albacares*, that lacked a left pectoral fin (Fig. 1). The fish was frozen and was brought to the Inter-American Tropical Tuna Commission, La Jolla, CA, for study by W. H. Bayliff.

Pectoral fins provide virtually all hydrodynamic lift in scombrids and are essential for stable and efficient swimming at sustained speeds (Magnuson 1973, 1978). A specimen with only one pectoral fin raises questions on what ways the fish might have compensated for an asymmetrical decrease in hydrodynamic lift and how the presence of only one pectoral fin might have affected its locomotion. We examined the fish to determine what may have caused fin loss and whether morphology was noticeably altered in a manner suggesting some compensation.

Skin in the area where the left pectoral fin should have been was thin, smooth, and silvery in appearance (Fig. 1). There was neither a trace of pectoral fin remnants nor a skin groove for it, suggesting the fin had never formed. On the other hand, the appearance of the skin and the presence of variably sized scales in the area around the normal fin position is compatible with a healed wound, and we thus could not rule out the possibility that the fin had been bitten off cleanly.

Methods

The specimen was X-rayed and maximum body height and width measured. We measured and traced its median fins, caudal keel, pectoral fin, and both pelvic fins, and estimated their surface areas with a planimeter. The same body and fin measurements were made on similarly sized, preserved yellowfin tuna in the Scripps Institution of Oceanography Fish Collection (SIO). Morphometric data were compared with values derived from the literature (Gibbs and Collette 1967; Fierstine and Walters 1968; Magnuson 1973, 1978; Magnuson and Weininger 1978, app. II). Although some of the specimen's caudal rays were bent (Fig. 1), all rays were present, and the fin was extended to a more natural position before its span was measured and area (which was well defined) traced. Also, to avoid measurement errors noted by Fierstine and Walters (1968) and Magnuson (1978), care was taken not to overextend caudal fins during span measurement.

Density of the thawed fish was determined by water displacement (density = wet weight/displacement volume). The right and left pectoral girdles were then removed and the gas bladder was inspected. Transverse sections were cut (see Graham et al. 1983), concentric myotomal rings on the right and left sides were counted, and red and white muscle were weighed for each section.

Results

The abundance of comparative morphometric and anatomical data for the yellowfin tuna permits a nearly complete assessment of the morphologic and hydrodynamic status of the one-finned specimen. The length (L; 36.5 cm)/weight (861.2 g) relationship and the density (1.080 $g \cdot mL^{-1}$) agree with values published for yellowfin tuna by Magnuson (1973, tables 1, 4). Also, the maximum thickness value (i.e., max. height + max. width/2 = 21.6% L) is within the range (20.5-23.0% L) measured for four SIO specimens (L from 28.5 to 42.5 cm) and near the value given by Magnuson (1973, table 7, 22.3% L). Finally, the point of maximum body thickness in the study fish (39.7% L) and that of SIO fish (36-40% L) are near Magnuson's value of 41.2% L (for fish from 28 to 45 cm L).

The dorsal fin of this fish is normal in shape, with 13 spinous rays, a maximum height of 3.5 cm and a surface area of 9.5 cm^2. The second dorsal fin is

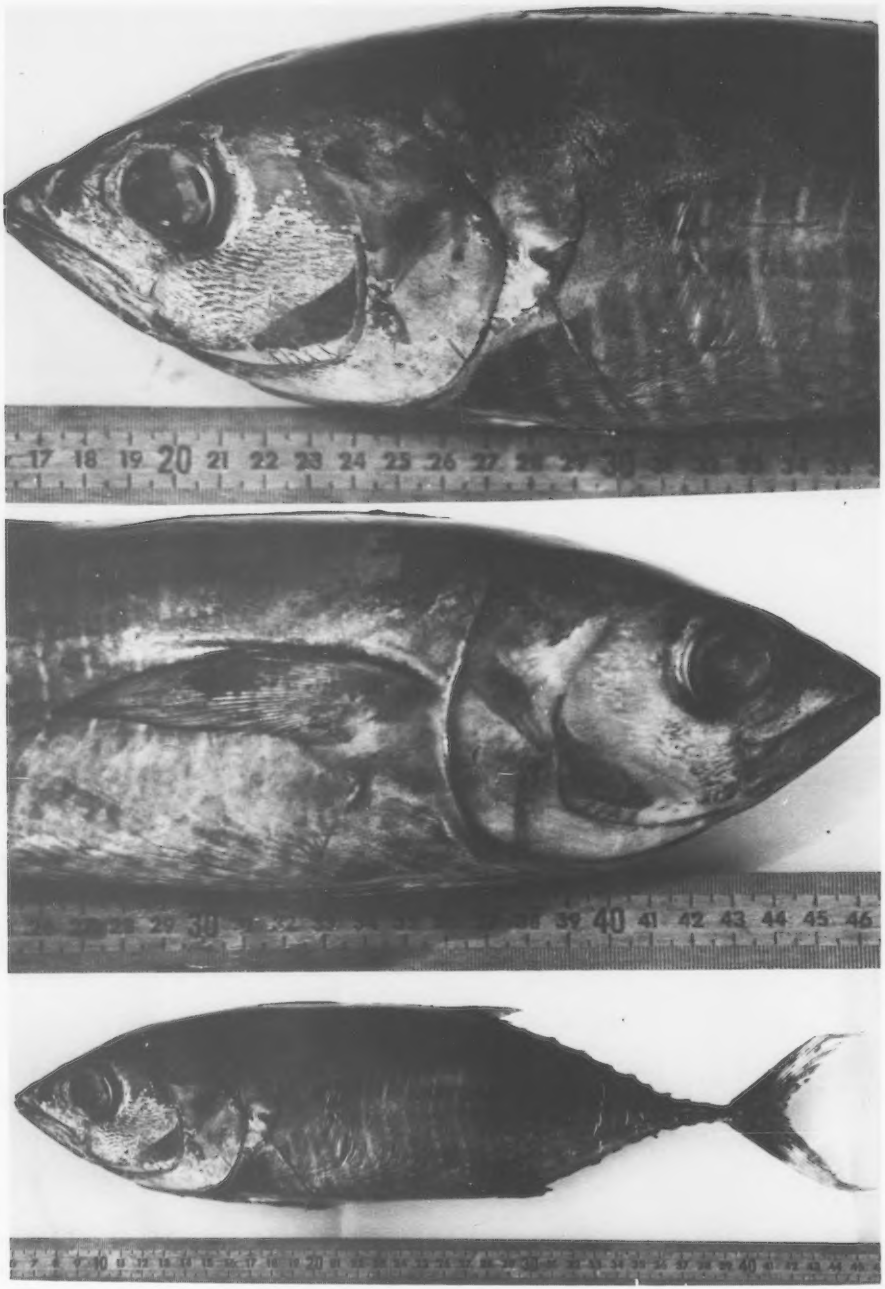

FIGURE 1.—Left- and right-side close-ups and a full-length, left-side photo of the *Thunnus albacares* with only one pectoral fin.

1 cm high and has an area of 2.0 cm^2. The anal fin is also 1 cm high and has an area of 2.2 cm^2. The combined total surface area of both sides of the second dorsal and anal fins is 8.4 cm^2, which is larger than predicted (7.2 cm^2) by the Magnuson and Weininger equation (1978, app. II). The total number of second dorsal and anal fin rays and dorsal and ventral finlets agrees with that for other yellowfin tuna (Gibbs and Collette 1967, table 1).

Table 1 compares caudal keel area and caudal and right pectoral fin dimensions of the study specimen and seven SIO fish of differing L. Also shown are values calculated for several of the same parameters using allometric equations for *T. albacares* (Magnuson 1978, table X; Magnuson and Weininger 1978, app. II). The caudal keel area of the one-finned fish (6.2 cm^2) is smaller than the value expected from the equation (6.7 cm^2) but is well within (i.e., 93%) the range of variation (77-102%) seen in the SIO specimens (Table 1). Comparison of the measured and the equation-derived caudal data for the one-finned fish with the same set of values for the next smallest (32.5 cm) and largest (37.0 cm) SIO fish indicates that the caudal fin of the one-finned fish has a slightly smaller span but larger area than would be expected for its L. This is further reflected in its aspect ratio (AR; 4.63), which is lower than that of any of the SIO specimens. This lower value probably does not represent an artifact of preservation because in the other material caudal span and area increased directly with L. There is also general agreement between the measured and calculated values for each, showing that neither preservation nor measurement protocols affected caudal fin data. As would be expected from the underlying formulae, caudal AR calculated from the equations increases with L. However, among the measured data, there is no correlation between AR and L. It is also noteworthy that both the mean and predicted AR values of all of these small yellowfin (5.64, 5.34, Table 1) are in good agreement but well below the summary range (6.8-7.2) given for larger *T. albacares* by Magnuson (1978, table IX). This serves to emphasize that while AR may differ between species of scombrids (Magnuson 1978), it also varies within each species as a function of body size.

Both the length and area of the right pectoral fin of the one-finned fish are much less than those of the 37 cm SIO specimen (Table 1). When measured and computed pectoral fin areas are compared, there is good agreement between both values for the 37 and 42.5 cm L fishes but not for the 36.5 cm L one-

TABLE 1.—Comparative caudal and right pectoral fin measurements for the one-finned yellowfin tuna (36.5 cm L) and seven specimens of different lengths (L) from the SIO collection. Data for each fish includes the actual measured values (m) and values calculated (c) from equations in the footnotes (Magnuson and Weininger 1978, app. II).

Fork length (cm)	Caudal keel	Caudal fin			Right pectoral fin		
					Length		
	Area[1] (cm^2)	Span[2] (cm)	Area[3] (cm^2)	Aspect ratio[4]	(cm)	(%L)	Area[5] (cm^2)
25.8 m	2.7	9.5	12.7	7.11	5.63	(21.8)	6.7
c	3.1	6.8	9.9	4.67			9.4
28.5 m	3.8	8.0	12.3	5.20	6.00	(21.0)	5.3
c	3.8	7.7	12.1	4.90			11.3
31.5 m	3.7	9.0	15.8	5.13	7.71	(24.5)	11.1
c	4.8	8.8	14.8	5.23			13.5
32.5 m	4.8	10.0	15.7	6.37	7.25	(22.3)	10.6
c	5.2	9.1	15.8	5.24			14.2
[6]36.5 m	6.2	10.0	21.6	4.63	7.50	(20.5)	12.8
c	6.7	10.5	20.0	5.51			17.5
37.0 m	5.3	11.0	21.6	5.60	9.67	(26.1)	17.8
c	6.9	10.7	20.6	5.56			17.9
40.0 m	8.5	12.5	25.4	6.15	10.40	(26.0)	[7]14.3
c	8.3	11.7	24.1	5.68			20.6
45.0 m	8.8	12.2	30.3	4.91	11.00	(25.9)	25.3
c	10.8	13.5	30.7	5.92			25.4
m				$\bar{x}$, SE 5.64, 0.30			
c				$\bar{x}$, SE 5.34, 0.15			

[1]Caudal keel area = $0.00198\ L^{2.28}$.
[2]Caudal span = $-2.27 + 0.35\ L$
[3]Caudal area = $0.013\ L^{2.04}$
[4]Aspect ratio = $Span^2/area$
[5]Pectoral fin area = $0.116\ L^{1.78}/4$.
[6]One-finned fish.
[7]Fin was torn.

finned fish. In general, application of the pectoral area equation to the smaller SIO fish (Table 1) does not result in close correspondence between estimated and observed areas, suggesting that the relationship derived from larger individuals does not fit smaller yellowfin tuna. The relative length of the pectoral fin in yellowfin tuna changes abruptly with size. In fish between about 35 and 42 cm L, pectoral fin length should normally be about 25% L (Gibbs and Collette 1967, fig. 26). This contrasts with the value for the one-finned fish of 20.5% L.

The left pectoral girdle is present, but clearly abnormal in gross examination. The posttemporal is reduced in overall size; the upper (pterotic) fork is somewhat reduced and lower (epiotic) fork weakly developed and without a flattened articular surface. The rear margin of the supracleithrum is eroded, and the lateral surface rough. The cleithrum is almost as large as that of the right side, but the lateral groove for muscle attachment is reduced, and the upper process that normally curves out over the scapula is absent. The scapula is a block of bone without an articular facet for the first pectoral ray, and the scapular foramen is represented by a slit in the lateral surface. The coracoid is much reduced posteriorly, and its reduced lower process is tightly applied to the cleithrum so that the interosseus space is almost absent. The pectoral actinosts may be represented by a small lump of bone that is tightly attached to the scapula. A number of bone chips were embedded in the tissue overlying the pectoral girdle. The postcleithra appear to be essentially normal.

Elements in the left side of the pelvic girdle are larger and have a different orientation from those of the right. Also, the left pelvic fin is both smaller in area and shorter than the right (Fig. 2). Pelvic fin lengths and areas in the one-finned fish are left 2.9 cm, 3.2 cm^2; right 3.5 cm, 4.7 cm^2. Comparable values for the 37.0 L SIO fish are left 3.5 cm, 4.5 cm^2; right 3.7 cm, 4.9 cm^2. X-rays showed that the centra of vertebrae 19 and 20 are abnormal (Fig. 3). They lie parallel to one another and overlap by about 80% in the horizontal axis. There is considerable erosion of the adjoining surfaces of the two centra and their neural and haemal spines are displaced. This deformity, together with the reduced left pelvic fin, the absence of a left pectoral fin, and a deformed left pectoral girdle, suggests the presence of a congenital malformation.

As would be expected from our density findings, the gas bladder of the one-finned fish was small (17 × 5 mm, length × diameter), but about the same size as that of other yellowfin tuna (Magnuson 1973, 1978). Finally, we found no differences in the left and right body myotomes. The total red muscle was estimated to be 6.7% of wet weight, which is within the 95% confidence limits of the value reported for yellowfin tuna (5.2-7.8%) by Graham et al. (1983).

FIGURE 2.—Anterior ventral view showing the reduced size of the left pelvic fin.

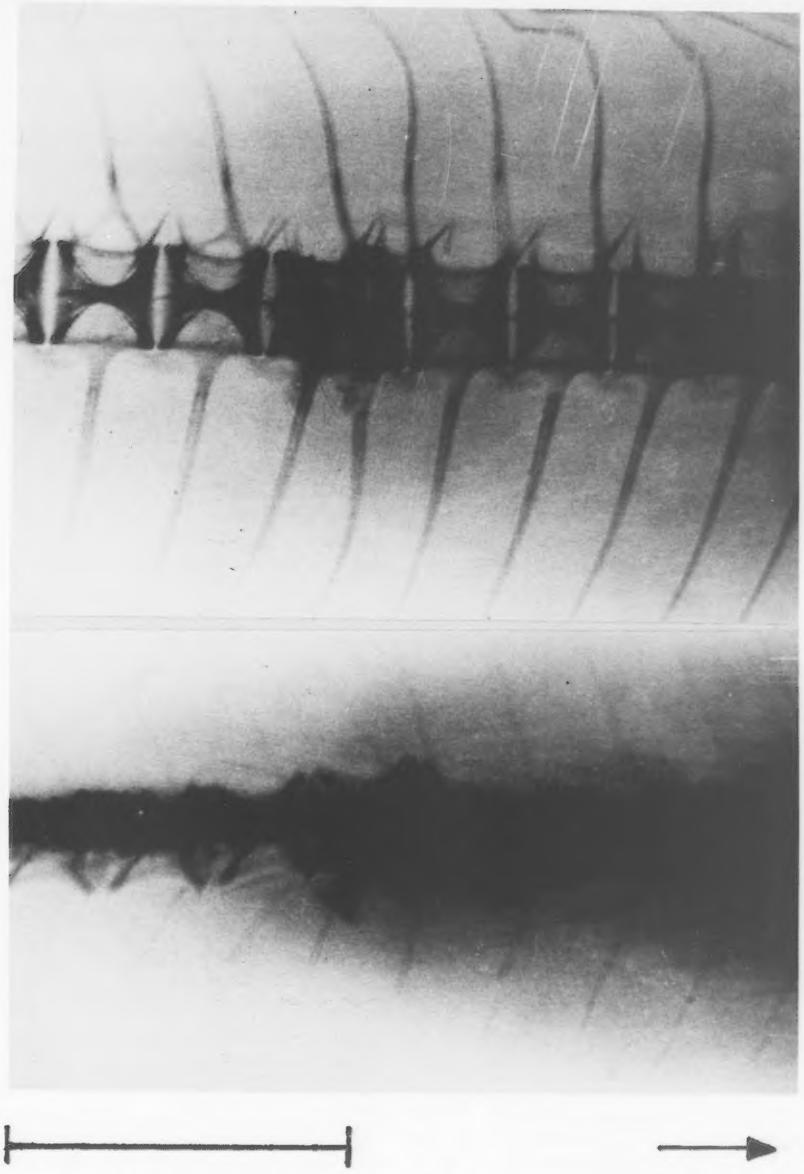

FIGURE 3.—Top: Right-side X-ray of the vertebral column showing the impacted vertebrae and the neural and haemal spine displacement. Bottom: Dorsal X-ray of the same vertebrae. Arrow indicates anterior. Scale is 2.5 cm.

Discussion

Our study suggests that congenital defects led to the absence of a left pectoral fin, the formation of a small right pectoral and left pelvic fins, and to the impaction of two vertebrae. A smaller caudal span may also be a result of such defects. On the basis of age studies (Uchiyama and Struhsaker 1981) we estimate that this fish (36.5 L) was about 9 mo old when captured. (But, because of the vertebral damage, the fish is shorter than it should be and 9 mo is a conservative age estimate.) Thus in spite of significant locomotory handicaps, this fish had been swimming and feeding effectively at the time it was taken by hook and line.

Morphological comparisons with SIO specimens and with equation-derived values for similarly sized yellowfin tuna did not indicate any major structural differences in the one-finned fish that can be interpreted as having facilitated its swimming. However, since the absence of one pectoral fin doubtlessly affects the minimum speed required for hydrostatic equilibrium, the horizontal stability, and the maneuverability of a tuna, it is instructive to consider how the loss might have been compensated. Magnuson (1973, 1978) has amply demonstrated the role of the paired fins in providing lift and reducing minimum equilibrium speed. Total lift (L_t) is calculated as

$$L_t \text{ (dynes)} = M[1 - \frac{\rho_e}{\rho_f}(g)], \quad (1)$$

where M is fish wet weight, ρ_e is seawater density, ρ_f is fish density, and g is the acceleration of gravity (980 cm·sec^{-2}). The amount of lift needed by the one-finned fish (M = 861 g, ρ_f = 1.08, ρ_e = 1.02 at 25°C) is 47,203 dynes.

The minimum speed for hydrostatic equilibrium U_{100} is determined by

$$U_{100} = \left[\frac{L_t}{\rho_e/2\,(C_{L_f}A_p + C_{L_k}A_k)}\right]^{1/2}, \quad (2)$$

where C_L is the coefficient of lift for the pectoral fins (p) and caudal keel (k) and A_p and A_k are their respective areas (Magnuson 1973). Pectoral fin lift area includes both fins and the flat section of body between them (Magnuson 1978, fig. 4). This can be calculated from an allometric relationship (Magnuson 1973, table 4).

$$A_p = 0.0609\ L^{1.87}, \quad (3)$$

and, for a 36.5 cm L yellowfin, A_p = 50.8 cm^2. With this value, a measured keel area (Table 1) of 6.2 cm^2, and assuming a lift coefficient of 1.0 for both surfaces (Magnuson 1973, table 4) the calculated (Equation (2)) minimum speed for a 36.5 cm yellowfin tuna is 40.3 cm·s^{-1}. The same calculation for the one-finned fish (A_p = 25.4 cm^2) yields a minimum speed of 54.1 cm·s^{-1}, a 34.3% increase. The one-finned fish would need to swim faster, and thus expend more energy. Its higher speed would also probably have required it to make continuous velocity and position changes in order to keep pace with a school of, on average, similarly sized and thus slower swimming yellowfin tuna.

Alternatively the fish might have assumed a pitched (i.e., head up) swimming mode in an attitude such that its body surface would have contributed to hydrodynamic lift by having a positive angle of attack relative to the direction of motion, and the C_L of the caudal keel would be increased (Magnuson 1978). Of course this would result in increased pressure drag and require more swimming power, but it might have enabled the fish to swim more slowly.

Under any conditions, it seems likely that this fish was not highly maneuverable and would have difficulty remaining upright (i.e., not rolling to the left). It, of course, could not use its left pectoral for braking and left turns, and its left pelvic fin, which would also contribute to these actions, was less effective than normal because of its small size. Tunas normally accelerate with their first dorsal, pectoral, and pelvic fins appressed (Magnuson 1978), but as this fish slowed and needed lift it would have likely began to roll to its left as soon as its right pectoral fin was extended. This could be countered somewhat by its dorsal fin, but the necessity for unilateral use of the right pectoral fin should have always resulted in some amount of leftward roll and a tendency to turn to the right. Both the sharpness of the turn and the net upward or downward spiral movement of the fish would depend upon the degree of fin extension and swimming velocity.

Finally, to compensate for the tendency to roll it is possible that the fish habitually swam with its body tilted as much as 80° to the right. In this position it would retain the largest possible pectoral lift area and might gain sufficient additional lift from the dorsal, second dorsal, anal fins and the body surface to more than compensate for loss of keel lift. It is noteworthy that the second dorsal and anal fin areas of this fish are larger than predicted (see above). The fish would be able to roll from its side to an upright position merely by extending its pectoral fin a bit

farther. Also, side swimming would place both pelvic fins in a position where they could facilitate rapid left (now ventral) turns while possibly adding lift.

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CHROMOSOMAL ANALYSIS OF ALBACORE, *THUNNUS ALALUNGA*, AND YELLOWFIN, *THUNNUS ALABACARES*, AND SKIPJACK, *KATSUWONUS PELAMIS*, TUNA

Chromosomal analysis is being used as part of an investigation of the population stock structure of the North Pacific albacore, *Thunnus alalunga*. There is a growing body of evidence (Brock 1943; Laurs and Lynn 1977; Laurs and Wetherall 1981; Laurs 1983) that North Pacific albacore are not as homogeneous as usually assumed (Clemens 1961; Otsu and Uchida 1963). Results from recent tagging studies suggest that northern and southern substocks constitute the North Pacific albacore population and that these proposed substocks have different migratory patterns (Laurs and Nishimoto 1979[1]; Laurs 1983). Laurs and Wetherall (1981) also found that the growth rates were significantly different in the two proposed substocks. In addition, the differences in growth rate are consistent with differences in length frequencies of albacore caught in commercial fisheries off North America (Brock 1943; Laurs and Lynn 1977).

In this paper we report results from chromosomal analysis using C-banding for albacore (from the proposed North Pacific southern substock) and compare them with similar results obtained for yellowfin, *Thunnus alabacares*, and skipjack, *Katsuwonus pelamis*, tuna. We demonstrate that there is a chromosomal basis for placing the albacore and the yellowfin tuna in the genus *Thunnus* and that recognizable chromosomal differences exist between the genera *Thunnus* and *Katsuwonus*. These findings corroborate the taxonomy of the albacore and the yellowfin and skipjack tuna based on comparative anatomy (Gibbs and Collette 1967; Collette 1978).

The results reported here are from part of a larger study, which is helping us to evaluate if genetic heterogeneity exists in the North Pacific albacore population. Information on chromosome characteristics is scarce for fishes, and to our knowledge this is the first time chromosome analyses have been reported for scombrid fishes.

Materials and Methods

All blood samples were collected from freshly caught fish either aboard the NOAA RV *David Starr Jordan* (August 1983) or aboard fishing boats

[1]Laurs, R. M., and R. N. Nishimoto. 1979. Results from North Pacific albacore tagging studies. U.S. Dep. Commer., Natl. Mar. Fish. Serv., SWFC Admin. Rep. LJ-79-17, 9 p.

(October-November 1983). Because albacore have a high titer of red blood cells (Alexander et al. 1980), it was expedient to separate the lymphocytes from the erythrocytes. The lymphocytes were isolated from the blood on a density gradient of ficoll-sodium diatrizoate solution using a modification of the technique developed by Boyum (1968), which is specific for the concentration of lymphocytes. We found that it was necessary to isolate the lymphocytes and place them in culture within a couple of hours after blood samples were collected. The ficoll gradient procedure was not successful using undiluted heparinized blood that was retained for more than a few hours.

Two albacore, three skipjack tuna, and four yellowfin tuna were sampled. All fish were juveniles which have virtually no sexual dimorphic characteristics, and no sex determinations were made. The estimated fork lengths of the fish ranged from 65 to 85 cm for albacore, 80 to 120 cm for yellowfin, and 45 to 55 cm for skipjack.

From each fish, an 8-10 mL sample of blood was withdrawn via sterile intracardial puncture into a syringe coated with 1,000 units/mL of heparin. Two mL aliquots of blood were pipetted into each of the four 15 mL centrifuge tubes, and 4 mL of cell culture medium[2] was added. The mixture was centrifuged at 20 *g* for 5 min, and the white cells and plasma were transferred to another centrifuge tube. This procedure for the separation of the plasma and white cell mixture was repeated three times following the suggestions given by Blaxhall (1981).

Five mL of the white cell-plasma mixture were layered over 3 mL of ficoll-sodium diatrizoate solution and centrifuged at 572 *g* for 30 min. The overlaying plasma was removed carefully with Pasteur pipets, and the lymphocytes below were transferred to a culture tube containing 5 mL of marine teleost cell culture medium (Michael and Beasley 1973). This procedure resulted in an erythrocyte free culture of lymphocytes having a higher mitotic index. The cultures were incubated at 25°C for 3-5 d, at which time they were terminated and the cells harvested. The techniques for chromosomal analysis were patterned after those of Nowell (1960) for mammals because tuna are also endothermic (Graham and Dickson 1981). This work is an extension of the procedures developed by Kelly and Laurs (1983[3]).

Prior to harvesting the cells, 0.5 μg colcemid was added to 5 mL of culture medium and incubated for 2 h at 25°C. The culture was then centrifuged for 5 min at 180 *g* and the supernatant was replaced with 5 mL 0.075 M KCl for 10 min. The culture tubes were centrifuged again for 5 min at 180 *g*, and the supernatant was replaced with 3 mL of freshly prepared cold fixative which consists of 3 parts methyl alcohol to 1 part glacial acetic acid and mixed for 1 h. The tubes were again centrifuged at 180 *g* for 5 min, decanted, and fixed. The cell pellet plus 0.5 mL of fixative was retained for slide preparation.

Precleaned slides dipped in methanol and then in deionized water were used for slide preparations. Two drops of cell suspension were placed on the slide and 4 drops of fixative were immediately added. The slide was dried on a slide warmer at 37°C and stored at room temperature for 24-72 h prior to C-banding. The C-banding procedures were patterned after the work of Pardue and Gall (1970) and Arrighi and Hsu (1971).

In preparation for C-banding, the slides were placed in 0.2 N HCl for 15 min at 37°C, rinsed in deionized water, treated with saturated $Ba(OH)_2$ at room temperature for 7 min, and rinsed in deionized water. They were then immediately dipped again in 0.2 N HCl for 10 s and rinsed in deionized water. After the final rinsing the slides were incubated in 2× sodium chloride-sodium citrate solution at 60°C for 90 min and then stained for 90 min in Giemsa diluted with 1:10 Sorenson's buffer pH 6.8. Suitable metaphase figures were photographed at 1,008× magnification using a Zeiss[4] microscope equipped with a phase planapochromat 63/1.4 oil immersion lens.

Results

Chromosome Numbers

Kelly and Laurs (fn. 3) found that the diploid number of chromosomes for albacore was 48. We have confirmed this observation and have found that the diploid numbers for yellowfin and skipjack tuna are also 48. The modal frequencies of about 90 cells containing 48 chromosomes were 82.2% for albacore, 92.6% for yellowfin, and 80.5% for skipjack. Kelly and Laurs also observed that 85% of albacore cells had 48 chromosomes. Two polyploid cells with

[2]RPMI-1640 Sigma Cat. No. R6504.

[3]Kelly, Raymond M., and R. Michael Laurs. 1983. Summary of methods developed for investigations of albacore chromosomes and of findings made on number of chromosomes. Unpubl. field and laboratory notes and results (April 1983). [Raymond M. Kelly, School of Medicine, University of California, La Jolla, CA; R. Michael Laurs, National Marine Fisheries Service, NOAA, La Jolla, CA.]

[4]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

96 chromosomes were observed in skipjack, and one polyploid cell with 96 chromosomes was observed in albacore. No polyploid cells were observed in yellowfin.

Chromosome Morphology

The albacore and the yellowfin and skipjack tuna were observed to have the same diploid chomosome number; however, their karyotype differed with respect to chromosome morphology. In this study, the chromosome pairs were arranged according to the morphology index (M), developed by Giannelli and Howlett (1967), which is obtained by dividing the length of the total haploid chromosome set p + q by the arm ratio (q/p). Based on our evaluation of 256 metaphase cells (Table 1), we found that the chromosome morphology of the yellowfin (Fig. 1) is more similar to that of the albacore (Fig. 2) than the skipjack (Fig. 3). The differences in chromosome morphology were most apparent in the three largest pairs of chromosomes (Table 1). The morphology index (M) places the metacentric and submetacentric chromosomes of the albacore and yellowfin in the number 1 and 2 positions respectively. Chromosome 3 of the albacore is also submetacentric while chromosome 3 of the yellowfin is referred to as subtelocentric. The subtelocentric category is used to describe chromosomes in which the centromeres are displaced more towards the telomere when compared with submetacentrics. The metacentric chromosome of the albacore was consistently larger than the metacentric of the yellowfin. The remaining 42 chromosomes were telocentric in the albacore and yellowfin. All of the chromosomes of the skipjack were telocentric.

C-Banding Patterns

C-banding determinations were done to differentiate individual chromosome characteristics among the three species of tunas (Table 2). The centromeric regions of most of the chromosomes of all three species contained C-band constitutive heterochromatin. However, there were differences in the intensities of staining on comparable chromosomes among the three species. Intercalary C-banding was observed only in the skipjack tuna and there was variability in terminal banding among the three species.

In the albacore all chromosomes, except pair 10, showed C-banding in the centromeric regions with intense, prominent bands notably apparent in chromosome pairs 2 and 3 (Fig. 2). Terminal banding was restricted to chromosome pair 1 which had obscure C-bands on one arm of each homologue. No intercalary C-banding was observed in the albacore. There were some minor differences in the C-banding patterns between albacore and yellowfin tuna. In the yellowfin, the centromeric regions of all chromosomes were banded, the intensity of the banding in the centromeric region was uniform

TABLE 1.—Classification of chromosome morphology for albacore and yellowfin and skipjack tuna.

Chromosome number	Albacore	Yellowfin	Skipjack
1	metacentric	metacentric	telocentric
2	submetacentric	submetacentric	telocentric
3	submetacentric	subtelocentric	telocentric
4-48	telocentric	telocentric	telocentric

TABLE 2.—Summary of C-banding characteristics for albacore and yellowfin and skipjack tuna.

Location of bands	Albacore	Yellowfin	Skipjack
Centromeric region	Present on all chromosomes except pair 10; intensely prominent on pairs 2 and 3	Present on all chromosomes with uniform prominent intensity	Present on all chromosomes except pairs 10 and 19, great variability in intensity most prominent on pairs 1, 3, 4, 7, and 18
Terminal bands	Present on one arm of each homologue on pair 1; weakly developed	Weakly developed on chromosome pairs 1, 3, 7, 8, 14, 15, 21, & 24	Notably prominent in pair 4
Intercalary	None present	None present	Present on all chromosome pairs except 17 and 24

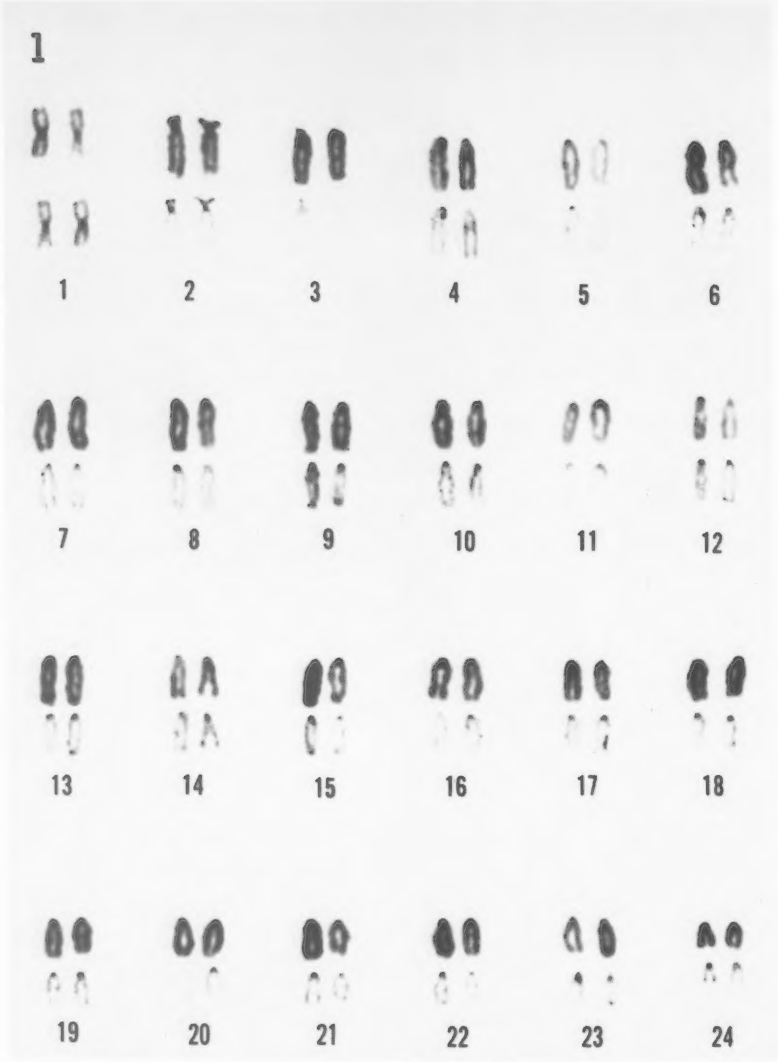

FIGURE 1.—Giemsa stained karyotype (upper row) and C-banding karyotype (lower row) of the same yellowfin tuna.

among all chromosomes, and terminal banding was weakly developed on eight pairs of chromosomes (Fig. 1). As in the albacore, no intercalary banding was observed in the yellowfin. The following significant differences were observed in the C-banding patterns between the skipjack and the other two species: 1) all chromosomes except 10 and 19 had C-banding in the centromeric region, 2) there was great variability in the intensity of staining in the centromeric region, 3) terminal banding was notably prominent in chromosome pair 4, and 4) there were intercalary bands on all chromosomes except pairs 17 and 24.

Discussion

Our results assist in understanding speciation processes that have occurred in the evolution of the

FIGURE 2.—Giemsa stained karyotype (a) and C-banding karyotype (b) from two different fish of the North Pacific albacore.

tuna. Gibbs and Collette (1967) proposed that seven species of tuna be included in the genus *Thunnus* on the basis of external morphological and internal anatomical characters. Our results demonstrate that there is a genetic basis for placing the albacore, *T. alalunga*, and the yellowfin tuna, *T. albacares*, in one genus *Thunnus* and the skipjack tuna, *Katsuwonus pelamis*, in a separate genus. These relationships are based on the assumption that closely related species will share certain karyotypic characteristics.

The determination that the albacore, yellowfin tuna, and skipjack tuna have the same number of chromosomes suggests that speciation of the genera of Thunnini might have occurred by intrachromosomal rearrangement as opposed to Robertsonian changes as hypothesized for the rainbow trout, *Salmo gairdneri* (Thorgaard 1976). If speciation had

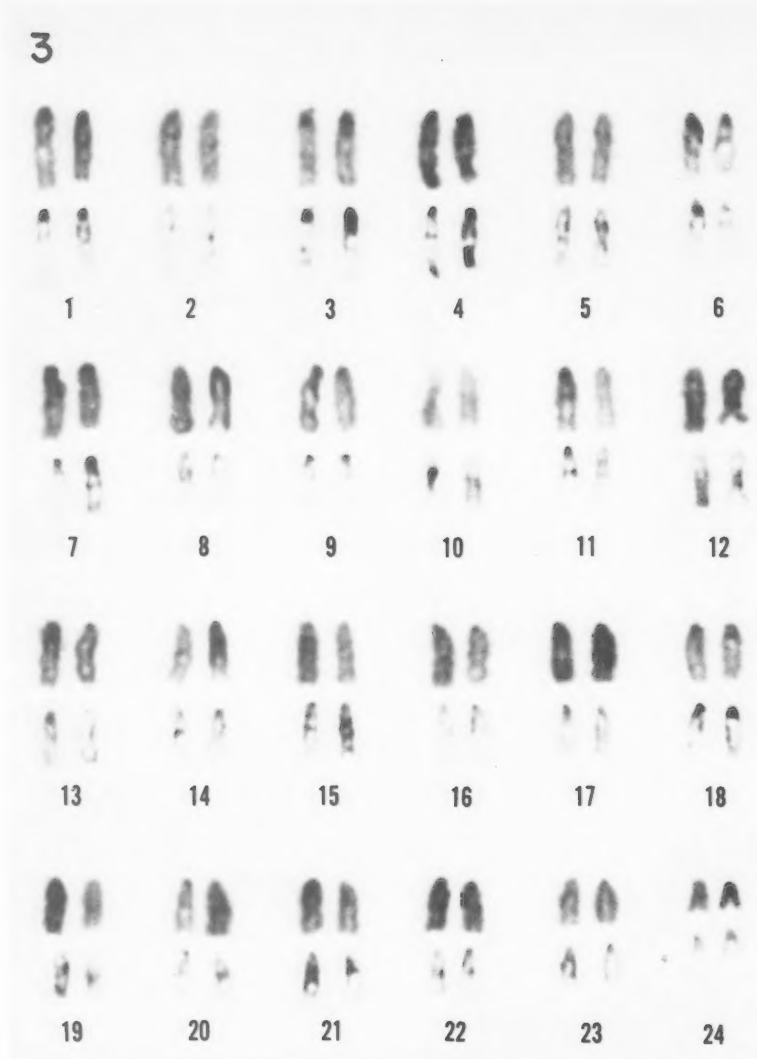

FIGURE 3.—Giemsa stained karyotype (upper row) and C-banding karyotype (lower row) of the same skipjack tuna.

involved a reduction in uniarmed chromosomes to form biarmed chromosomes, we would have expected to find a difference in the chromosome number between *Katsuwonus* and *Thunnus*.

It is probable that speciation within the genus *Thunnus* might also be related to chromosome rearrangement because the number of chromosomes is the same. Pericentric inversion is a type of intrachromosomal rearrangement that could result in the displacement of the centromere to convert a telocentric chromosome into a metacentric one. Zenzes and Voiculescu (1975) suggested that pericentric inversion was involved in the chromosomal organization of the brown trout, *Salmo trutta*. The extent to which this mechanism has been related to the speciation of genera *Thunnus* and *Katsuwonus* is

uncertain. However, the occurrence of terminal C-bands on chromosome 1 of the albacore and chromosomes 1 and 3 of the yellowfin tuna is consistent with the hypothesis that these biarmed chromosomes were derived from a uniarmed condition. Indeed, White (1951) believed that, in grasshoppers, telocentric chromosomes are more primitive than the metacentric condition. Absence of terminal bands on chromosomes 2 and 3 of the albacore and chromosome 2 of the yellowfin tuna does not preclude the suggested derivation of metacentric chromosomes. It is possible that in the metacentric chromosomes lacking terminal bands, centrometric heterochromatin either was not moved or was lost. It is also possible that chromosome rearrangement in the speciation of the albacore and yellowfin occurred through changes in the euchromatic portions of chromosomes. To test this hypothesis it will be necessary to use G-banding techniques (Rishi 1978) to conduct analysis of these portions of the chromosomes.

In contrast to the albacore and yellowfin tuna, the telocentric chromosomes of the skipjack tuna showed a variety of intercalary and terminal C-banding in addition to those of the centromeric regions. An interesting condition was the polymorphic terminal heterochromatic block that occurred in chromosome pair number 4 of the skipjack, but not in the albacore or yellowfin. While the four specimens of skipjack analyzed had this polymorphism, it is not possible to comment on the frequency with which it might occur in the population. This type of differential banding also occurs in other fishes as demonstrated by Zenzes and Voiculescu (1975) who observed a difference in the size of C-bands in *Salmo trutta*. The C-band polymorphism we observed in skipjack could be related to the sex determining mechanism of the fish. However, we do not have any information on the sex of the skipjack used in this study and most fish do not have heteromorphic sex chromosomes (Zenzes and Voiculescu 1975; Thorgaard 1976; Kligerman and Bloom 1977). An exception occurs in the eels which have highly heteromorphic sex chromosomes (Park and Grimm 1981).

Analysis of C-banding patterns associated with the morphological differences in chromosomes has permitted us to identify all of the chromosome pairs of the albacore, yellowfin tuna, and skipjack tuna. We have demonstrated that karyotype analysis may provide a chromosomal basis for placing albacore and yellowfin in *Thunnus* and skipjack in *Katsuwonus*. Although C-banding techniques did not allow a detailed evaluation of the *Thunnus* chromosomes, we believe that the use of multiple banding procedures could provide important information on the speciation and cytotaxonomy of the species of this commercially important genus. In addition, use of G-banding procedures will be an important next step in determining if genetic heterogeneity exists in the North Pacific albacore population.

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ABUNDANCE, SIZE, AND SEX RATIO OF ADULT SEA-RUN SEA LAMPREYS, *PETROMYZON MARINUS*, IN THE CONNECTICUT RIVER[1]

Populations of sea-run sea lampreys, *Petromyzon marinus*, occur in many rivers on the east coast of North America from Labrador to Florida (Bigelow and Schroeder 1953). The Connecticut River in the northeastern United States is believed to have the largest population (Beamish 1980). Although the historical, upstream range of the sea lamprey in the Connecticut River is not known, it probably was similar to American shad, *Alosa sapidissima*, which migrated 280 km upstream to Bellows Falls, VT (Moffitt et al. 1982).

Upstream migration of anadromous fish species in the Connecticut River main stem was first restricted in 1798 by the construction of Turners Falls Dam at km 197, and further in 1849 by the construction of Holyoke Dam at km 140. The first upstream fish passage facility for anadromous fish was a fish lift at Holyoke Dam that began operating in 1955. Until 1969 the sea lampreys using the fish lift were counted and either killed or thrown back. From 1969 to 1984, they have been passed upstream each year. Sea lampreys have also used the fish ladders that were completed in 1980 and 1981 at Turners Falls and Vernon Dams, respectively. With the completion of the fish ladder at Bellows Falls Dam in 1984, migrants now have access to 350 km of main-stem river and many additional tributaries (Fig. 1).

The present report summarizes the annual counts of sea lampreys from 1958 to 1984 at the two Holyoke fish lifts (a second fish lift was added in 1976). We also examined the sex ratio, total length, and weight of adults in 1981-82 and compared these characteristics with those of the population in the St. John River, New Brunswick. Beamish et al. (1979) sampled the St. John River population at km 140, at a fish lift located at Mactaquac Dam.

Methods

Sea lampreys that were lifted above the dam were counted each year from 1958 to 1984, except for the period from 1969 to 1974. From 1958 to 1968, sea lampreys were counted by personnel of the Holyoke Water Power Company (the owner of the dam), and

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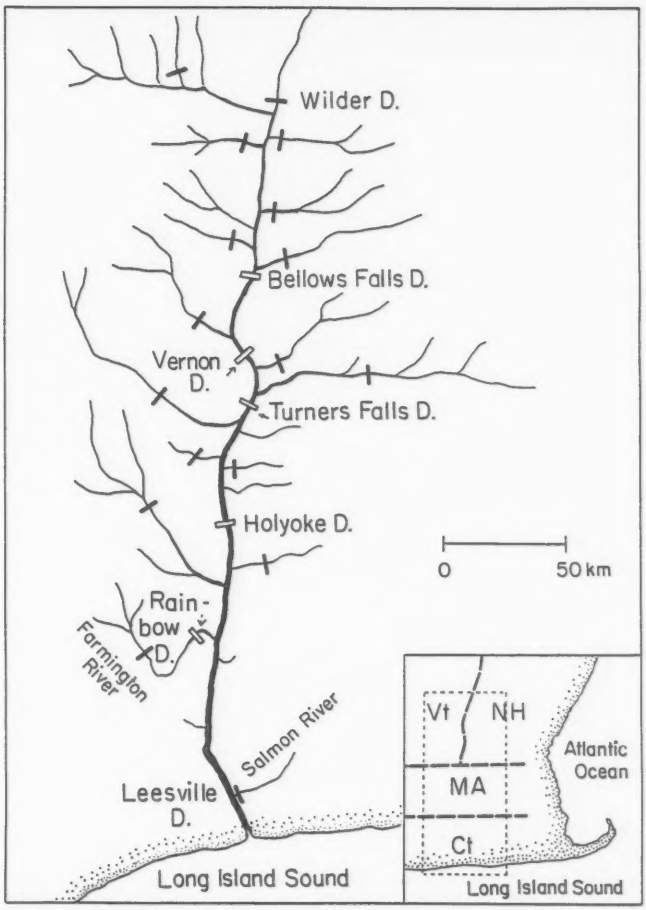

FIGURE 1.—Map of the Connecticut River showing the location of Holyoke Dam and the other dams with fishways on the lower 350 km of the main stem and major tributaries. Dams that sea lampreys can pass are designated by an open bar; dams they cannot pass are designated by a solid bar.

from 1975 to 1984, they were counted by personnel from either the Massachusetts Division of Fisheries and Wildlife or the Massachusetts Cooperative Fishery Research Unit. Until 1975, fish of all species were lifted, deposited into small carts, carried across the dam, and counted as they were released. Beginning in 1975, all fish were sluiced directly from the fish lift bucket into a large flume and were counted through a glass window in the side of the flume as they swam upstream. The accuracy of these counts has not been experimentally determined. However, the counts are probably very accurate because the sea lampreys are large and swim slowly through the flume.

We collected sea lampreys daily at the fish lift trap from 1 May to 10 June 1981, and from 10 May to 30 June 1982 for determination of total length (TL) and sex. The number of sea lampreys sampled each day was proportional to the number lifted the previous day. The number of sea lampreys lifted and (in parenthesis) the number collected follow: 0-50 (2); 51-100 (4); 101-200 (6); 201-400 (8); 401-800 (10); 801-1,000 (15); 1,001-2,000 (25); 2,001-3,000 (30); 3,001-5,000 (40); >5,000 (50). in both years, total

length was measured to the nearest millimeter and sex was determined by dissection. We determined the sex ratio for each day of the run to observe changes during the migration. In 1982 each sea lamprey was also weighed to the nearest gram. Chi-square tests were used to compare the sex ratios for differences from a 1:1 frequency. Student's t-test was used to compare the males and females for mean length and weight. We compared males and females for the length-weight relationship by calculating a separate regression for each sex using the logarithmic equation: $\log w = \log a + (b)(\log 1)$ (Ricker 1975).

Results and Discussion

Abundance

The numbers of sea lampreys lifted from 1958 to 1967 were relatively few, and probably reflected the inefficiency of the fish lift rather than a small population (Fig. 2). After the flume and second lift were added in 1975 and 1976, respectively, 22,000-53,000 adults have been passed upstream each year. The 53,000 counted in 1981 was the largest number ever passed at Holyoke and the largest run documented in any river. In 1981, 59% of the total run was lifted during the week of 24-30 May; and in 1982, 68% were lifted during the week of 28 May-3 June. Beamish (1980) reported that about 8,600 sea lampreys are lifted annually in the fish lift at Mactaquac Dam. He estimated the spawning populations in other northern streams at <8,000.

The sea lampreys that reach Holyoke Dam are only a portion of the total run, because several tributaries below the dam support populations (Whitworth et al. 1976). The sea lamprey population may increase as adults gain access to additional spawning and rearing habitat in headwater streams by using fish passage facilities constructed for Atlantic salmon, *Salmo salar*, and American shad (Moffitt et al. 1982). Thus, the restoration program designed primarily for Atlantic salmon and American shad is also restoring the sea lamprey to additional habitat. Since 1975, over 20,000 sea lampreys have been passed each year at Holyoke Dam and given access to new spawning and rearing habitat. The estimated life span of sea lampreys in the St. John River is estimated at 9-12 yr (Beamish and Potter 1975). Therefore, if the Connecticut River population returns to their natal stream and has a similar life cycle, and if the strength of the year classes after 1975 was enhanced by the additional rearing habitat above Holyoke, then beginning in

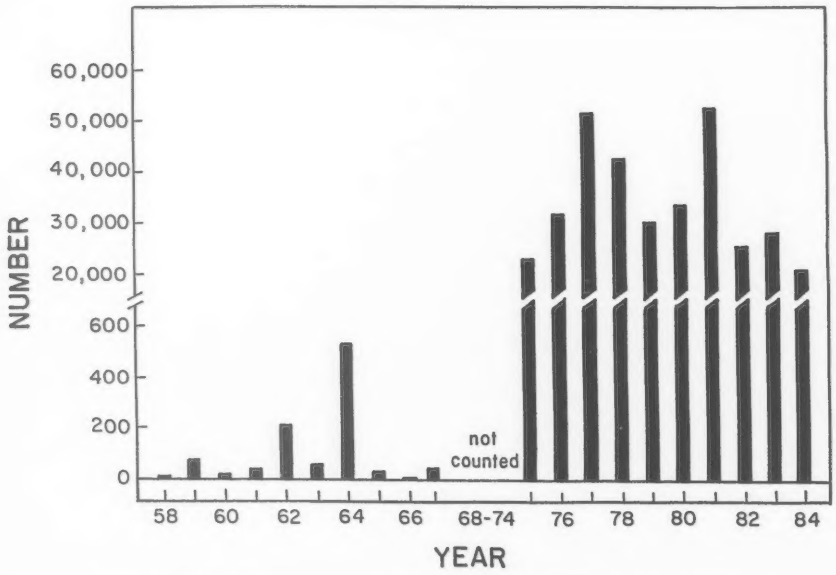

FIGURE 2.—Number of adult sea lampreys lifted in the Holyoke fish lifts each year, 1958-84.

1984 there should be increased returns of adults at Holyoke. The return of sea lampreys at Holyoke in 1984 was not a record return, but this could be due to the high discharge caused by the 50-yr flood that occurred in early June 1984, when most sea lampreys are lifted. If the sea lamprey population increases, the wound frequencies should increase on host species of marine and anadromous fish.

Sex Ratio

Sex ratios for both years were skewed from 1:1 in favor of males, but the ratio was only significant in 1982: in 1981, 56% were males (ratio: 1.3:1; $\chi^2 = 3.4$, $P > 0.05$; in 1982, 62% were males (ratio: 1.6:1; $\chi^2 = 11.6$, $P < 0.005$, Table 1). Sex ratios also changed during the spawning migration with the proportion of males increasing late in the run. The percent of males in the early and late periods were 55 and 59% in 1981 and 59 and 67% in 1982. The increase in the proportion of males was not significantly different from a 1:1 ratio in 1981, but the increase was significant in 1982 ($\chi^2 = 7.6$:$P < 0.01$). Applegate (1950) found that males in landlocked sea lamprey populations increased to about 75% in the late part of the run. The reason for this phenomenon is unknown.

Males are the most abundant sex in stable populations of sea-run and landlocked sea lampreys. Beamish et al. (1979) reported 55% males (ratio: 1.36:1) in nearly mature adults in the St. John River in 1974-77 (Table 1). Davis (1967), who collected anadromous sea lampreys for 5 yr from Barrows Stream, ME, reported a male:female ratio of 1.9:1; however, the sample size was very small ($N = 66$). Potter et al. (1974) found an excess of males in landlocked sea lamprey (ratio: 1.26:1). The sex ratio in stable populations (where males are more abundant than females) is different from the ratio in populations from the upper Great Lakes, where an excess of females is typical of populations being eradicated or controlled (Smith 1971). Sex ratios in sea lampreys also vary with cycles of abundance (Wigley 1959; Smith 1971), and temperature and nutrition may differentially affect growth and survival of male and female ammocoetes (Hardisty 1954).

TABLE 1.—Mean total length and weight (SE in parenthesis), and percent males in sea lampreys sampled at Holyoke Dam, Connecticut River, compared with samples collected from the Mactaquac Dam, St. John River.

Dam & year	N	Mean length (cm) Male	Mean length (cm) Female	Mean length Male	Mean length Female	Percent male
Holyoke						
1981	464	71.3 (2.8)	71.5 (2.9)	—	—	56
1982	404	71.4 (2.7)	71.1 (3.6)	[1]794 (8.2)	[2]806 (12.01)	62
Mactaquac[3]						
1974-77	341	72.4 (4.7)	72.9 (5.1)	868 (18.1)	885 (18.3)	55

[1]249 males were weighed.
[2]155 females were weighted.
[3]Data from Beamish et al. (1979); ± 95% confidence limits in parenthesis.

Total Length and Weight

In 1981, 464 sea lampreys (0.9% of the number lifted) were measured for total length; in 1982 the number examined was 404 (1.5% of the number lifted). There was no significant difference between the mean length of males and females during either year or for both years (Student's t-test: $P > 0.05$, Table 1). Length of females and males ranged from 60 to 85 cm in both years.

The similarity in mean total length of adults in the consecutive spawning runs of 1981-82 suggests relative stability of the sea lamprey population. This differs greatly from the unstable sea lamprey populations in the Great Lakes where body length decreased from 1950's to 1960's—changes related to decreases in food supply and changes in the environment (Smith 1971).

The mean weight of females was not significantly different from the mean weight of males (Student's t-test: $P > 0.05$, Table 1). We determined the length-weight relationship by using the regression equations: $\log w = -3.42 \pm (2.21)$ (log 1), ($r^2 = 0.75$, $P < 0.01$) for females and $\log w = -3.11 \pm (2.10)$ (log 1), ($r^2 = 0.76$, $P < 0.01$) for males. There was no significant difference between the slopes of the regression lines, consequently we combined males and females ($N = 404$). Using the equation $y = b + mx$ or weight = b + (slope) (length), a highly significant correlation ($r^2 = 0.76$, $P < 0.01$) was found for the regression equation: weight = 521.9 + (0.23890) (length). The length-weight relationship is linear, rather than sigmoid, as it is in most fishes. Because the body is attenuate, the weight of sea lampreys does not increase as rapidly with length as it does in most other fishes. This relationship is less evident in females, possibly because of the additional weight of their eggs.

Generally, in landlocked populations, females are slightly heavier than males because of their high fecundity (Applegate 1950). We also found this was true. Although the sea lampreys at Holyoke Dam were similar in length to those in the St. John River,

the average weight of Connecticut River fish was considerably less (Table 1). The difference in average weight between sea lampreys in the two populations is not due to the difference in location of upstream sampling sites, but possibly to differences in energetic requirements, food supplies, or some aspect of the environment during the oceanic parasitic phase. A difference in weight between populations has previously been found in landlocked sea lampreys in the Great Lakes (Smith 1971).

Acknowledgments

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AN IMPROVED OTTER SURFACE SAMPLER

Field trials using a neuston sampler described by Sameoto and Jaroszynski (1969) revealed serious sampling problems associated with coastal waters of British Columbia. Due to extensive freshwater runoff in the vicinity of large rivers, sampling conditions including choppy surface waters of lowered salinity and vertically depressed distributions of near-surface larval and juvenile fishes. Under such conditions, the S-J sampler behaved erratically, throwing considerable spray, and, when adjusted to increase depth of tow, the body and control surfaces deformed at speeds in excess of 5 knots. The modifications described here reflect our objectives of improving performance, increasing durability, and ease of handling, without increasing costs other than those incurred by adding a flowmeter to provide quantitative catches. The complete unit is depicted in Figure 1.

Detailed Description

Sampler Box

Constructed of 1/8″ marine aluminum, this aluminum is folded into a body with one welded seam (Fig. 2). The leading edges are reinforced with 1/4″ aluminum for attaching the bridles and depressor. The square mouth opening was sized to accomodate 0.25 m^2 bongo nets having a circumference of 185 cm. Body dimensions are 46 × 46 × 60 cm.

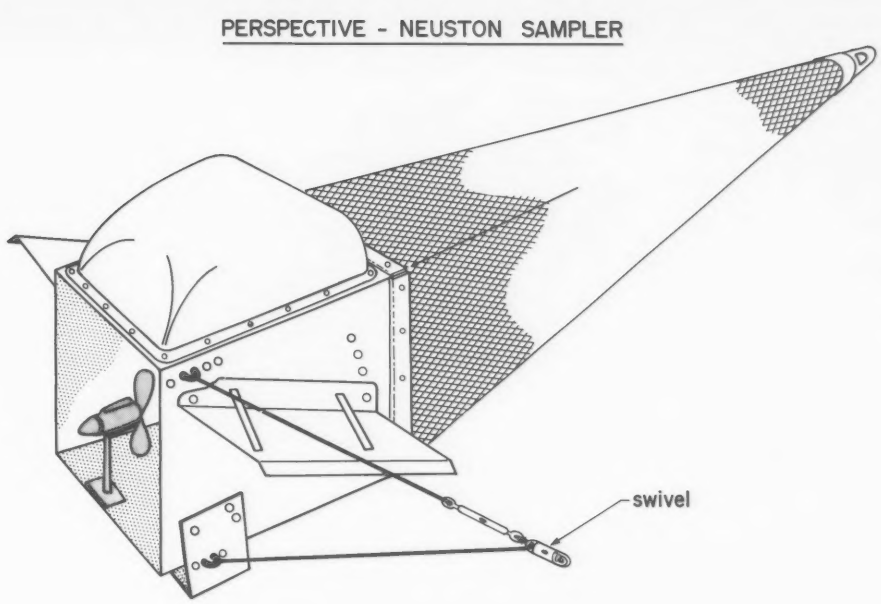

FIGURE 1.—Neuston sampler with net cod-end attached.

Net Attachment

We replaced the grommet and bolt-through net fastening system of the S-J sampler with an aluminum channel clamp (Fig. 2). Net slippage is prevented by sewing a 1/4″ rope into the net collar. Stainless steel bolts remain permanently attached to the sampler body so that, to mount or replace the net, it is merely slid over the box and the channel placed over the bolts and secured. One man can replace the net in 5 min.

Lateral Wings

Individual fins bolt directly to the sides of the body and are made of 1/8″ aluminum with the inside edge bent at 90° for an attachment face (Fig. 3). The outer edge is bent downward 15° to stiffen it and to reduce side slippage under tow. The wings pivot on a bolt anteriorly and are adjusted through a series of holes in the sampler body (Figs. 1, 2).

Depressor

Bolted directly to the body and adjusted as for the wings (Figs. 1, 2), the depressor is made from 1/4″ marine aluminum bent at right angles on either end for attachment (Fig. 3). It serves also as the lower towing point and stiffens the body.

Tow Points

The sampler is adjusted in relation to the towing vessel by a stainless steel turnbuckle on the upper bridle (roll aspect), and by selecting the lower tow point (depressor) and upper tow point (leading top corner of the body) from a series of holes (Figs. 1, 2, 3). The tow point fastening is a threaded U-bolt, fastened on both sides of the sampler frame (Fig. 3).

Flotation

A streamlined float constructed of fiberglassed, polyurethane foam which bolts to the upper face of the body (Figs. 1, 2). At neutral buoyancy the sampler floats with the mouth opening just below the water surface. As with the S-J sampler, vertical positioning under tow is the balanced outcome of downward depressor force and lift from the lateral fins. These adjustments are made to maintain an 8-10 cm headspace of air in the sampler while under tow.

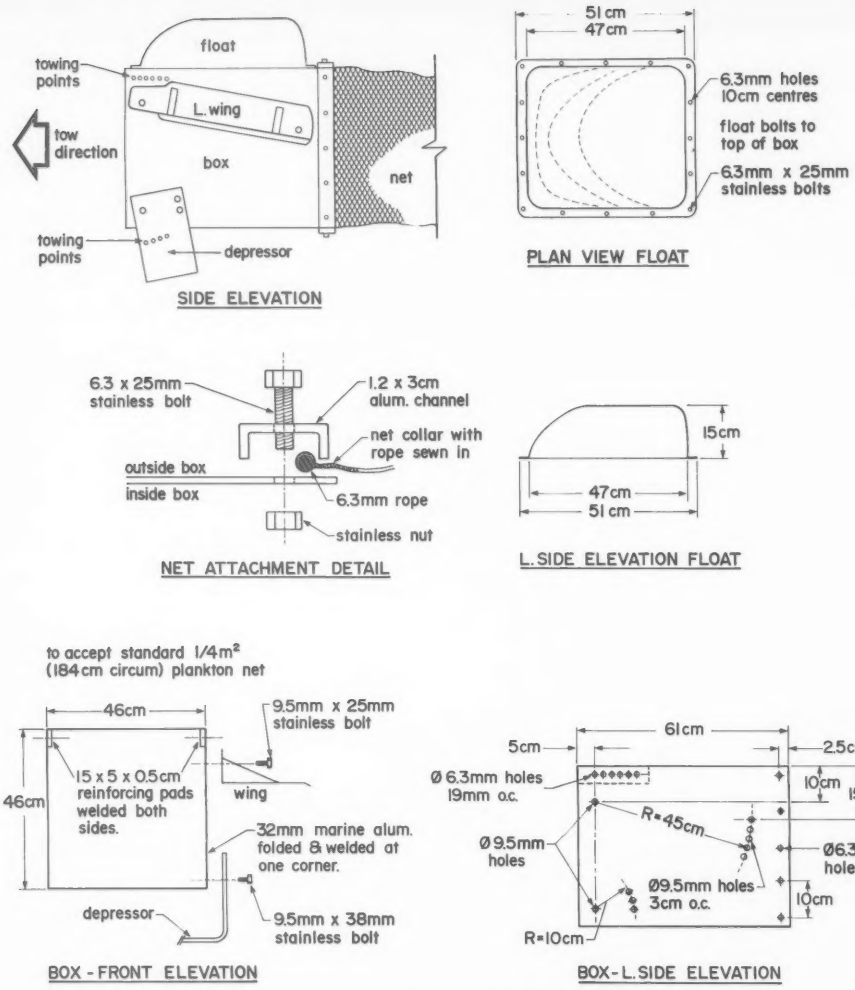

FIGURE 2.—Scale drawings of the sampler body and float, and net attachment detail.

Flowmeter

A General Oceanics meter is attached inside the body by means of a hinged strut which folds forward to facilitate reading the meter (Figs. 1, 3). The meter is free-pivoting in the horizontal plane and offset 17 cm from the center of the mouth opening.

Evaluation

This modified version of the otter neuston sampler has been used extensively since 1981, offshore to Station Papa (Mason et al. 1983) and in inside waters under all weather conditions, including a full gale. It performs best when towed into or across the wave direction at 4-6 knots. At higher speeds, disturbance due to backsplash from the fins and bridal may cancel out potential advantage of further increase in tow speed. Sampling efficiency is deemed to be relatively high when using a 500 μm mesh net at night. Catches of juvenile fishes in the Strait of Georgia are quantitatively comparable with those

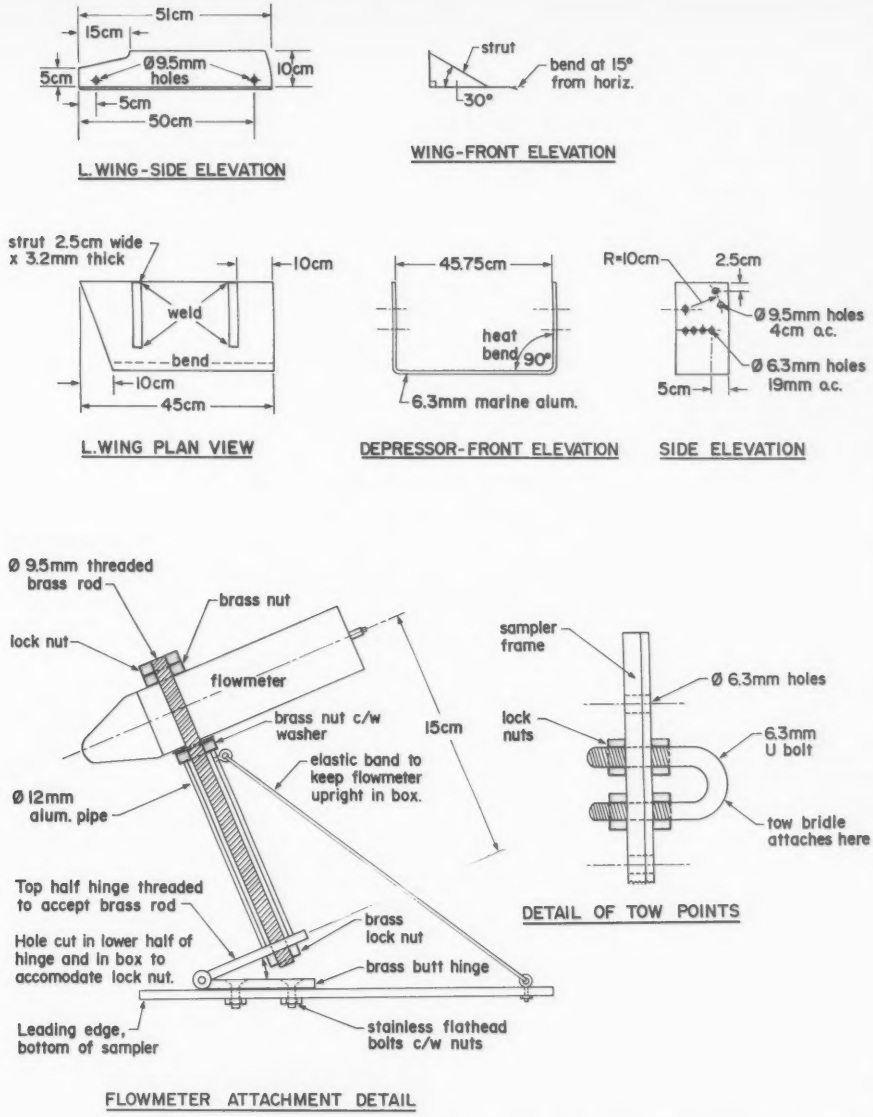

FIGURE 3.—Scale drawings of the depressor and wings, and tow point and flowmeter details.

made with a large volume, two-boat surface trawl as employed by Barraclough et al. (1966). We found no significant difference (student's *t*-test) between mean total catch (12.9 and 12.1 fish/100 m^3) for nine taxa common to both gears in eight pairs of tows made locally in the Strait of Georgia, British Columbia, during March-April. Among the fish sampled by this gear in offshore and shelf waters are juvenile Pacific salmon to 14 cm, Pacific saury to 25 cm, juvenile sablefish, rockfish, greenlings, and squid, in addition to the routine catches of ichthyoplankton and general zooplankton.

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MORPHOLOGICAL EVIDENCE FOR STARVATION AND PREY SIZE SELECTION OF SEA-CAUGHT LARVAL SABLEFISH, *ANOPLOPOMA FIMBRIA*

One of the major causes of larval mortality is starvation, this being related to the patchiness of food resources (Hunter 1981). While starvation has been induced under laboratory conditions [e.g., herring, *Clupea harengus*, and plaice, *Pleuronectes platessa* (Ehrlich et al. 1976); northern anchovy, *Engraulis mordax* (O'Connell 1976); jack mackerel, *Trachurus symmetricus* (Theilacker 1978, 1981)], starved larvae have rarely been observed in nature (northern anchovy, O'Connell 1980; jack mackerel, Theilacker 1986). Various methods have been used to characterize starvation in fish larvae, including condition factor (Blaxter 1971), chemical analyses (Ehrlich 1974), histological analyses (Umeda and Ochiai 1975; O'Connell 1976, 1980; Theilacker 1978, 1986), and morphological analyses (Shelbourne 1957; Nakai et al. 1969; Ehrlich et al. 1976; Theilacker 1978, 1981, 1986). While histological and chemical analyses are based on qualitative changes in tissues that result from starvation, their methodologies require special preservation techniques, negating their application to samples preserved without these techniques in mind. To characterize starvation in samples that have not been specially preserved, measures of morphology and/or condition factor are more appropriately applied. In the present study, in the absence of special preservation techniques, the occurrence of starvation in sea-caught larval sablefish, *Anoplopoma fimbria*, was examined using morphological measures.

The sablefish inhabits the continental shelf of the North Pacific Ocean and is the subject of an intensifying fishery off the west coast of North America, yet little is known about the early life history of the species. Recent evidence obtained off Canada suggests that sablefish spawn in water deeper than 300 m, with spawning activity peaking in February. Eggs (1.8-2.2 mm in diameter) descend while developing, and hatching probably occurs at depths in excess of 400 m (Mason et al. 1983). Although size at hatching and the size at first feeding have not been clearly defined, Mason et al. (1983) reported collecting recently hatched larvae of 5-6 mm. After hatching, larvae ascend to surface waters and become neustonic (Kendall and Clark 1982[1]). Juveniles apparently remain in shallow water until they mature. Beyond reports of distribution (Kendall and Clark fn. 1; Clark 1984[2]) and descriptive work (e.g., Kobayashi 1957; Ahlstrom and Stevens 1976), studies of larval and early juvenile sablefish have concentrated on aging and growth (Boehlert and Yoklavich 1985; Shenker and Olla in press).

Our aim in the present study was to detect the possible occurrence of starvation in larval sablefish collected off Washington and Oregon during April and May 1980 (Kendall and Clark fn. 1), using selected morphological measurements to determine variability in larval condition. Further, to elucidate the possible relationship between larval condition and feeding requirements, prey size-selection and diet were analyzed.

Methods

Sablefish larvae were collected by using a 0.5 m neuston net (Sameoto and Jaroszynski 1969) with 0.505 mm mesh, towed for 10 min from the RV *Tikhookaenskiy*, during the first cooperative U.S.-U.S.S.R. ichthyoplankton survey off the Washington and Oregon coast in 1980 (Kendall and Clark fn. 1). Larvae from stations 20, 24, 25, 34, 38, 50,

[1]Kendall, A. W., and J. Clark. 1982. Ichthyoplankton off Washington, Oregon and Northern California, April-May 1980. Processed Rep. 82-11, 44 p. Northwest and Alaska Fisheries Center, National Marine Fisheries Service, NOAA, Seattle, WA 98112.

[2]Clark, J. B. 1984. Ichthyoplankton off Washington, Oregon and Northern California, May-June 1981. Processed Rep. 84-11, 46 p. Northwest and Alaska Fisheries Center, National Marine Fisheries Service, NOAA, Seattle, WA 98112.

54, 70, and 71 (Fig. 1), collected between 22 April and 4 May 1980, formed the basis for this study. All larvae were preserved in 10% Formalin[3] at sea. After sorting, larvae were switched into 5% Formalin, where they remained until their examination in 1983.

The following body measurements were recorded: standard length (SL), head length (HL), eye diameter (ED), body depth at pectoral (BD.P), and body depth at anus (BD.A) (after Theilacker 1981). Standard length was measured to the nearest 0.1 mm. All other measurements were made to the nearest 0.05 mm using an ocular micrometer. Because body proportions change dramatically with size of larvae, it was necessary to restrict any comparisons to samples which were not statistically different in terms of the distribution of SL values. Also, to minimize ambiguities attributable to slight differences in size, comparisons of body measurements were made using a ratio of the body measurement to SL (e.g., HL/SL) as well as the absolute measurement (mm). Because a number of larvae were damaged prior to the time measurements were made (e.g., eyes were missing, the gut was separated from the body) the sample size (n) varied within a station. To classify larval condition, statistical comparisons of the body measurements were made using the Mann-Whitney test (Zar 1974), a nonparametric rank procedure.

Food particle-size selection was examined by measuring the widths of prey items ingested by 84 larvae from stations 24, 34, 50, 70, and 71. Soft-bodied prey items were not measured due to the difficulty in accurately assessing their effective width. All measurements were made using an ocular micrometer at 40×. Prey widths were originally plotted for five size classes of larvae: 8.2-12.5, 12.6-16.5, 16.6-20.5, 20.6-24.5, and 24.6-28.5 mm SL. The prey-size selection curve of larvae 12.6-16.5 mm closely approximated the curve of larvae 16.6-20.5 mm, and so these size classes were combined. Similarly, the curves of larvae 20.6-24.5 mm and 24.6-28.5 mm were essentially superimposed one upon the other, and as a result these size classes were also combined. This yielded three functional sablefish size classes for particle-size analysis: 8.2-12.5, 12.6-20.5, and 20.6-28.5 mm SL.

The incidence of empty guts was recorded, and diet was analyzed in terms of numerical percent composition and frequency of occurrence of copepod nauplii.

[3]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

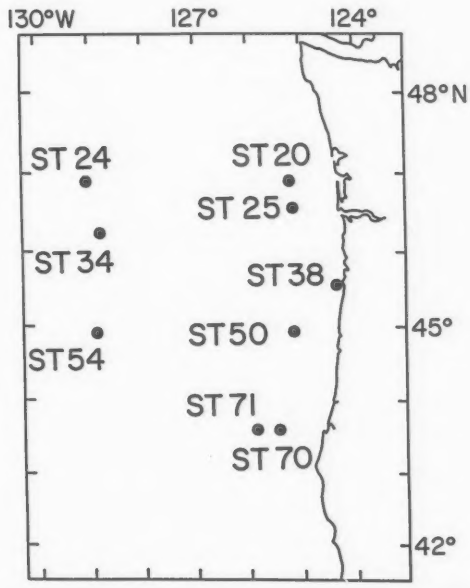

FIGURE 1.—Map of the Washington and Oregon coast where larval sablefish were collected in 1980.

Results

Morphological Measurements

Out of a total of 56 larvae collected at station 25, 48% (27 larvae) appeared emaciated, in marked contrast to larvae collected at all other stations. This emaciated condition, which we interpreted as evidence of starvation, was present in 82% of the larvae <12.5 mm SL (27 out of 32) collected at this station but was absent in fish larger than 12.5 mm SL. To test whether this interpretation, which was based on a gross visual examination of these larvae, was statistically verifiable, the morphology of the emaciated larvae from station 25 was compared with larvae of the same size from stations 20, 24, 34, 38, 50, 54, 70, and 71. The size range, 8.2-12.5 mm SL, was selected as the broadest range over which the distributions of SL values of these two groups were equivalent, and excluded the two smallest larvae collected at station 25 from the comparisons. Significant differences were observed in seven of eight body measurements, indicating that distinct differences were present in the larvae from station 25 when compared with larvae of similar size from all other stations (Table 1).

TABLE 1.—A comparison of median values of body measurements of *Anoplopoma fimbria* larvae from station 25 with larvae from stations 20, 24, 34, 38, 50, 54, 70, and 71. The size range was 8.2-12.5 mm SL.

	Station 25	Stations 20, 24, 34, 38, 50, 54, 70, and 71	P[1]
Standard length, SL (mm)	10.0	10.25	>0.20
95% Confidence Interval, C.I.	(9.2-10.4)	(10.0-10.5)	
n[2] =	25	118	
Head length, HL (mm)	1.5	2.1	<0.001
95% C.I.	(1.4-1.8)	(2.0-2.1)	
HL/SL	0.165	0.200	<0.001
95% C.I.	(0.147-0.177)	(0.194-0.206)	
n =	25	114	
Eye diameter, ED (mm)	0.7	0.85	<0.001
95% C.I.	(0.6-0.7)	(0.8-0.9)	
ED/SL	0.069	0.082	<0.001
95% C.I.	(0.066-0.073)	(0.081-0.084)	
n =	23	113	
Body depth at pectoral, BD.P (mm)	1.0	1.3	<0.001
95% C.I.	(0.9-1.15)	(1.3-1.3)	
BD.P/SL	0.109	0.128	<0.001
95% C.I.	(0.098-0.118)	(0.125-0.131)	
n =	13	100	
Body depth at anus, BD.A (mm)	1.0	1.2	<0.005
95% C.I.	(0.7-1.2)	(1.15-1.25)	
BD.A/SL	0.104	0.116	>0.10
95% C.I.	(0.082-0.139)	(0.112-0.118)	
n =	11	84	

[1]P = probability that body measurements of station 25 larvae were equivalent with larvae from stations 20, 24, 34, 38, 50, 54, 70, and 71, as determined by the Mann-Whitney test.
[2]The sample size was not constant within each group because some larvae were damaged prior to the time measurements were made (e.g., some had lost eyes, the gut was separated from the body).

Analysis of Gut Contents

Examination of the gut contents of larvae <12.5 mm SL provided further evidence as to the starved condition of the larvae at station 25. At this station 75% of the larvae (24 out of 32) had no food in their guts, and 9% (3 larvae) had ingested 2 or fewer prey items. In addition to being empty, the guts of larvae collected at station 25 were shrunken, which is reflective of poor feeding conditions (Nakai et al. 1969). At all other stations the incidence of empty guts for larvae <12.5 mm SL was <1%, as was the incidence of larvae ingesting 2 or fewer prey items.

Circumstantial evidence as to the cause of starvation comes from food analyses. It was apparent that while sablefish larvae selected increasingly larger prey as they grew larger, the minimum size of prey eaten did not increase appreciably. By examining the widths of all prey items ingested by larvae of different lengths (Fig. 2), three general patterns emerged: 1) Larvae 8.2-12.5 mm SL principally ingested the narrowest prey (0.01-0.10 mm in width), 2) larvae 12.6-20.5 mm SL ingested slightly larger prey (0.11-0.20 mm in width), and 3) sablefish 20.6-28.5 mm SL primarily ingested the largest prey (0.21-0.30 mm in width), although they also ingested a broad range of prey sizes.

Copepod nauplii were the dominant small prey, and were all <0.20 mm wide. They accounted for 88.3% of the diet (by number) of small larvae (≤12.5 mm). Based on prey-size selection alone (Fig. 2), it appears that copepod nauplii may have also contributed substantially to the diet of larvae 12.6-20.5 mm SL, but not to the diet of fish 20.6-28.5 mm SL. Dietary analysis confirmed this, with nauplii comprising 26.9% of the diet of larvae 12.6-20.5 mm, but merely 1.4% of the diet of fish 20.6-28.5 mm SL.

Considering the relative importance of copepod nauplii in the diet of larvae 12.6-20.5 mm SL and the fact that this size class continued to ingest nauplii although capable of ingesting larger prey, the frequency of occurrence of copepod nauplii in the guts of these larvae was examined at each station as inferential evidence of the abundance or availability of copepod nauplii (Table 2). At station 25 only 27% of larvae 12.6-20.5 mm SL ingested nauplii compared with 60-100% at all other stations; the low frequency of occurrence of nauplii in guts of these larvae at station 25 was obtained even though no guts were empty. These data indicate that copepod nauplii may not have been abundant or

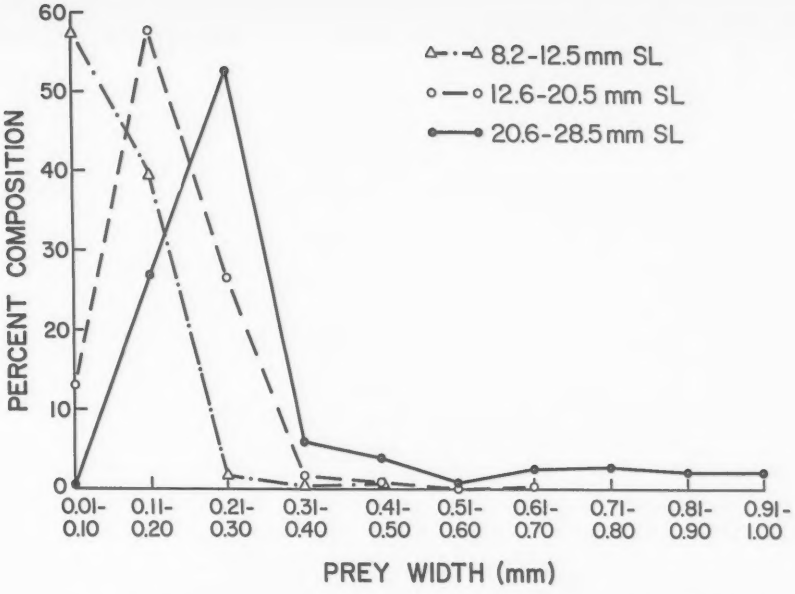

FIGURE 2.—The size of prey selected by larval sablefish, plotted for three size classes of larvae: 8.2-12.5 mm SL (n = 43), 12.6-20.5 mm SL (n = 25), and 20.6-28.5 mm SL (n = 16).

TABLE 2.—Frequency of occurrence of copepod nauplii found in the guts of larval sablefish, by size class and station.

	Station number								
Size class	20	24	25	34	38	50	54	70	71
≤12.5 mm	38/38	6/6	[1]7/32	9/9	32/32	6/6	15/16	10/10	11/12
	100%	100%	22%	100%	100%	100%	94%	100%	92%
12.6-20.5 mm	6/10	2/2	4/15	8/8	11/11	1/1	3/3	10/11	2/3
	60%	100%	27%	100%	100%	100%	100%	91%	67%

[1]This includes 24 larvae ≤12.5 mm SL with empty guts.

readily available at station 25, with the high incidence of starvation at this station suggesting a cause-and-effect relationship between these two factors.

Discussion

There is no definitive way of discerning whether the sablefish larvae that we categorized as starving had starved to the "point of no return". To ascertain whether sea-caught larvae have starved beyond recovery requires rearing larvae from eggs in the laboratory under different feeding regimes, and using these as standards of comparison for sea-caught specimens. Unfortunately, this has been done in only a few cases. For example, O'Connell (1976) established histological criteria for starvation under laboratory conditions for the northern anchovy. These criteria were then employed to identify starving larvae collected in the Southern California Bight (O'Connell 1980). The proportion of starving larvae was estimated to be 8%, for larvae <7.5 mm SL, with this representing 40% of the daily rate of mortality. In a more recent and comprehensive study, Theilacker (1986) utilized both histological and morphological criteria (Theilacker 1978, 1981) to examine starvation of sea-caught first-feeding jack mackerel in the Southern California Bight. She determined that starvation varied with habitat. In the open ocean, the number of larvae <3.5 mm dying

of starvation per day was 57-70%, whereas only 6-12% of the first-feeding larvae collected near islands and banks were starving.

Until techniques are developed for rearing sablefish from eggs, we are limited to utilizing comparisons of sea-caught larvae to infer the importance of starvation in the early life history of this species. While starving larvae were observed at only one station, our finding confirms that sablefish larvae do encounter suboptimal environmental conditions in the sea. However, neither the transience nor geographic extent of this phenomenon can be assessed in the absence of an intensive sampling scheme designed specifically to answer these questions.

Although definitive plankton composition data are lacking, the occurrence of starving larvae at station 25 appears to reflect a paucity of copepod nauplii. While appropriate prey concentrations (Laurence 1974; Lasker 1975; Houde 1978), particle size (Lasker 1975; Hunter 1981), and prey species composition (Lasker 1975; Scura and Jerde 1977) all relate to the survival and growth of marine fish larvae, not all larvae are able to maintain associations with suitable prey patches. Lasker (1975) emphasized the transient nature of optimal feeding conditions in the sea, noting that northern anchovy larvae which had been associated with a good feeding patch (a bloom of *Gymnodinium splendens* that persisted for 18 d) would probably die of starvation after a wind storm broke up the bloom. Patchiness of food resources has also been suggested by the station-to-station variability in growth rates of northern anchovy (as determined from daily increments of otoliths) (Methot and Kramer 1979). Similarly, after monitoring larval development in both good and bad plankton patches, Shelbourne (1957) reported that a scarcity of appropriate food resulted in a deterioration of the physical condition of plaice larvae.

Where morphological measurements of larvae are concerned, changes in body measurements which result from handling and preservation techniques must be considered. Net abrasion results in mechanical damage to the larvae (Blaxter 1971) as well as shrinkage (Blaxter 1971; Theilacker 1980), with the amount of shrinkage depending on whether death preceded fixation (Blaxter 1971), and the extent of handling (Theilacker 1980). The type of fixative used (Theilacker 1980), its concentration, salinity, and temperature (Hay 1982) also affect the degree of shrinkage. In the present case, shrinkage most likely occurred during the 3 yr these larvae were held in Formalin. However, absolute lengths may not be critical to evaluating the significance of our findings, and the differences that were seen between stations could not have resulted simply from differences in shrinkage. This was clear from the qualitative differences in gut appearance seen between stations (i.e., shrunken and empty guts versus guts filled to distention). Further, since the sablefish larvae we examined were all caught and preserved during the same cruise, we assumed that whatever shrinkage that may have resulted from handling and preservation techniques is constant throughout the samples.

Larval fishes are limited in the prey that they consume by their ability to capture and process it. As they grow, larvae become very successful predators, caused in part by an increase in mouth size. As a result, the size of prey selected increases as development proceeds. Prey width was used to examine prey-size selection because prey width appears to be the critical dimension for the successful ingestion of oblong prey by larval fishes (Blaxter 1965; Arthur 1976; Hunter 1981). For sablefish, definitive shifts in the size of prey consumed occurred at about 12.5 and 20.5 mm SL. The diet of the larger larvae was more diverse than the diet of small larvae. This expansion of the range of prey selected is not uncommon (e.g., Hunter 1981) and is adaptive inasmuch as it enables larvae to ingest suboptimal prey items at times when optimal or preferred prey are not available. Smaller fish appear limited in the size of prey they can exploit. This limitation, combined with larvae $\leq$12.5 mm SL being associated with an unsuitable prey patch at station 25, may have been responsible for the high incidence of empty guts and starvation.

Acknowledgments

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NOTICES

NOAA Technical Reports NMFS published during last 6 months of 1985

Technical Report NMFS

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    - Analysis of various sources of pelagic shark catches in the Northwest and Western Central Atlantic Ocean and Gulf of Mexico with comments of other large pelagics. By Emory D. Anderson, p. 1-14, 3 figs., 17 tables.
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    - Introduction: an egg production method for anchovy biomass assessment. By Reuben Lasker, p. 1-3, 1 fig.
    - Biomass model for the egg production method. By Keith Parker, p. 5-6.
    - Parameter estimation for an egg production method of northern anchovy biomass assessment. By Susan Picquelle and Gary Stauffer, p. 7-15, 8 figs., 6 tables.
    - Sea survey design and analysis for an egg production method of anchovy biomass assessment. By Paul E. Smith and Roger P. Hewitt, p. 17-26, 4 figs., 8 tables.
    - The CalCOFI vertical egg tow (CalVET) net. By Paul E. Smith, William Flerx, and Roger P. Hewitt, p. 27-32, 5 figs., 1 table.
    - Procedures for sorting, staging, and ageing eggs. By Gary Stauffer and Susan Picquelle, p. 33-35.
    - Staging anchovy eggs. By H. Geoffrey Moser and Elbert H. Ahlstrom, p. 37-41, 2 figs.
    - A model for temperature-dependent northern anchovy egg development and an automated procedure for the assignment of age to staged eggs. By Nancy C. H. Lo, p. 43-50, 2 figs., 6 tables.
    - A protocol for designing a sea survey for anchovy biomass assessment. By Robert P. Hewitt, p. 51-53.
    - Sampling requirements for the adult fish survey. By Susan Picquelle, p. 55-57, 1 fig.
    - Spawning frequency of Peruvian anchovies taken with a purse seine. By Jurgen Alheit, p. 59-61, 1 table.
    - Preservation of northern anchovy in formaldehyde solution. By J. Roe Hunter, p. 63-65, 1 fig., 1 table.

Batch fecundity in multiple spawning fishes. By J. Roe Hunter, Nancy C. H. Lo, and Roderick J. H. Leong, p. 67-77, 6 figs., 5 tables.
Measurement of spawning frequency in multiple spawning fishes. By J. Roe Hunter and Beverly J. Macewicz, p. 79-94, 7 figs., 1 table.
Comparison between egg production method and larval census method for fish biomass assessment. By Roger P. Hewitt, p. 95-99, 2 figs., 1 table.

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LO, NANCY C. H. Modeling life-stage-specific instantaneous mortality rates, an application to northern anchovy, *Engraulis mordax*, eggs and larvae 395
SEN, A. R. Methodological problems in sampling commercial rockfish landings ... 409
POLOVINA, JEFFREY J. A variable catchability version of the Leslie model with application to an intensive fishing experiment on a multispecies stock 423
MATSUURA, YASUNOBU, and NELSON TAKUMI YONEDA. Early development of the lophid anglerfish, *Lophius gastrophysus* 429
SQUIRES, DALE. Ex-vessel price linkages in the New England fishing industry .. 437
LEBER, KENNETH M., and HOLLY S. GREENING. Community studies in seagrass meadows: A comparison of two methods for sampling macroinvertebrates and fishes 443

Notes

OXENFORD, HAZEL A., and WAYNE HUNTE. A preliminary investigation of the stock structure of the dolphin, *Coryphaena hippurus*, in the western central Atlantic 451
FORWARD, RICHARD B., JR., BLANCA ROJAS de MENDIOLA, and RICHARD T. BARBER. Effects of temperature on swimming speed of the dinoflagellate *Gymnodinium splendens* 460
GRAHAM, JEFFREY B., RICHARD H. ROSENBLATT, and DARCY L. GIBSON. Morphology and possible swimming mode of a yellowfin tuna, *Thunnus albacares*, lacking one pectoral fin 463
RATTY, F. J., Y. C. SONG, and R. M. LAURS. Chromosomal analysis of albacore, *Thunnus alalunga*, and yellowfin, *Thunnus albacares*, and skipjack, *Katsuwonus pelamis*, tuna 469
STIER, KATHLEEN, and BOYD KYNARD. Abundance, size, and sex ratio of adult sea-run sea lamprey, *Petromyzon marinus*, in the Connecticut River 476
MASON, J. C., and A. C. PHILLIPS. An improved otter surface sampler 480
GROVER, JILL J., and BORI L. OLLA. Morphological evidence for starvation and prey size selection of sea-caught larval sablefish, *Anoplopoma fimbria* 484
Notices 490

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